

Mangroves among the most carbon-rich forests in the tropics

Daniel C. Donato^{1*}, J. Boone Kauffman², Daniel Murdiyarso³, Sofyan Kurnianto³, Melanie Stidham⁴ and Markku Kanninen⁵

Mangrove forests occur along ocean coastlines throughout the tropics, and support numerous ecosystem services, including fisheries production and nutrient cycling. However, the areal extent of mangrove forests has declined by 30–50% over the past half century as a result of coastal development, aquaculture expansion and over-harvesting^{1–4}. Carbon emissions resulting from mangrove loss are uncertain, owing in part to a lack of broad-scale data on the amount of carbon stored in these ecosystems, particularly below ground⁵. Here, we quantified whole-ecosystem carbon storage by measuring tree and dead wood biomass, soil carbon content, and soil depth in 25 mangrove forests across a broad area of the Indo-Pacific region—spanning 30° of latitude and 73° of longitude—where mangrove area and diversity are greatest^{4,6}. These data indicate that mangroves are among the most carbon-rich forests in the tropics, containing on average 1,023 Mg carbon per hectare. Organic-rich soils ranged from 0.5 m to more than 3 m in depth and accounted for 49–98% of carbon storage in these systems. Combining our data with other published information, we estimate that mangrove deforestation generates emissions of 0.02–0.12 Pg carbon per year—as much as around 10% of emissions from deforestation globally, despite accounting for just 0.7% of tropical forest area^{6,7}.

Deforestation and land-use change currently account for 8–20% of global anthropogenic carbon dioxide (CO₂) emissions, second only to fossil fuel combustion^{7,8}. Recent international climate agreements highlight Reduced Emissions from Deforestation and Degradation (REDD+) as a key and relatively cost-effective option for mitigating climate change; the strategy aims to maintain terrestrial carbon (C) stores through financial incentives for forest conservation (for example, carbon credits). REDD+ and similar programs require rigorous monitoring of C pools and emissions^{8,9}, underscoring the importance of robust C storage estimates for various forest types, particularly those with a combination of high C density and widespread land-use change¹⁰.

Tropical wetland forests (for example, peatlands) contain organic soils up to several metres deep and are among the largest organic C reserves in the terrestrial biosphere^{11–13}. Peatlands' disproportionate importance in the link between land use and climate change has received significant attention since 1997, when peat fires associated with land clearing in Indonesia increased atmospheric CO₂ enrichment by 13–40% over global annual fossil fuel emissions¹¹. This importance has prompted calls to specifically address tropical peatlands in international climate change mitigation strategies^{7,13}.

Overlooked in this discussion are mangrove forests, which occur along the coasts of most major oceans in 118 countries, adding ~30–35% to the global area of tropical wetland forest over peat swamps alone^{4,6,12}. Renowned for an array of ecosystem services, including fisheries and fibre production, sediment regulation, and storm/tsunami protection^{2–4}, mangroves are nevertheless declining rapidly as a result of land clearing, aquaculture expansion, overharvesting, and development^{2–6}. A 30–50% areal decline over the past half-century^{1,3} has prompted estimates that mangroves may functionally disappear in as little as 100 years (refs 1,2). Rapid twenty-first century sea-level rise has also been cited as a primary threat to mangroves¹⁴, which have responded to past sea-level changes by migrating landward or upward¹⁵.

Although mangroves are well known for high C assimilation and flux rates^{16–22}, data are surprisingly lacking on whole-ecosystem carbon storage—the amount which stands to be released with land-use conversion. Limited components of C storage have been reported, most notably tree biomass^{17,18}, but evidence of deep organic-rich soils^{22–25} suggests these estimates miss the vast majority of total ecosystem carbon. Mangrove soils consist of a variably thick, tidally submerged suboxic layer (variously called 'peat' or 'muck') supporting anaerobic decomposition pathways and having moderate to high C concentration^{16,20,21}. Below-ground C storage in mangrove soils is difficult to quantify^{5,21} and is not a simple function of measured flux rates—it also integrates thousands of years of variable deposition, transformation, and erosion dynamics associated with fluctuating sea levels and episodic disturbances¹⁵. No studies so far have integrated the necessary measurements for total mangrove C storage across broad geographic domains.

In this study we quantified whole-ecosystem C storage in mangroves across a broad tract of the Indo-Pacific region, the geographic core of mangrove area (~40% globally) and diversity^{4,6}. Study sites comprised wide variation in stand composition and stature (Fig. 1, Supplementary Table S1), spanning 30° of latitude (8° S–22° N), 73° of longitude (90°–163° E), and including eastern Micronesia (Kosrae); western Micronesia (Yap and Palau); Sulawesi, Java, Borneo (Indonesia); and the Sundarbans (Ganges-Brahmaputra Delta, Bangladesh). Along transects running inland from the seaward edge, we combined established biometric techniques with soil coring to assess variations in above- and below-ground C pools as a function of distance from the seaward edge in two major geomorphic settings: estuarine/river-delta and oceanic/fringe. Estuarine mangroves ($n = 10$) were situated on large alluvial deltas, often with a protected lagoon; oceanic mangroves ($n = 15$) were situated in

¹USDA Forest Service, Pacific Southwest Research Station, 60 Nowelo St., Hilo, Hawaii 96720, USA, ²USDA Forest Service, Northern Research Station, 271 Mast Rd., Durham, New Hampshire 03824, USA, ³Center for International Forestry Research (CIFOR), PO Box 0113 BOCBD, Bogor 16000, Indonesia, ⁴USDA Forest Service, International Programs, 1099 14th street NW, Suite 5500W, Washington, District of Columbia 20005, USA, ⁵Viiikki Tropical Resources Institute (VITRI), University of Helsinki, PO Box 27, FIN-00014, Finland. *e-mail: ddonato@wisc.edu.

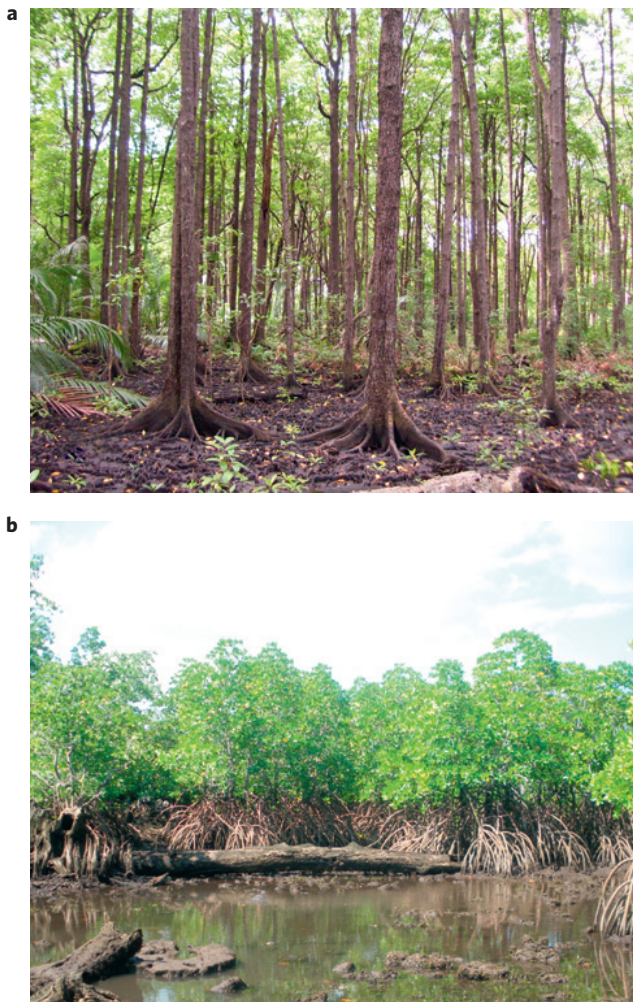


Figure 1 | Examples of Indo-Pacific mangroves. The sample included a broad range of stand stature, composition, and soil depth. **a**, Exemplary large-stature, high-density mangrove dominated by *Bruguiera*, Borneo, Indonesia (canopy height >15 m, canopy closure >90%, soil depth >3 m). **b**, Exemplary small-stature, low-density mangrove dominated by *Rhizophora*, Sulawesi, Indonesia (canopy height <4 m, canopy closure <60%, soil depth 0.35–0.78 m). Both estuarine and oceanic mangroves can exhibit both conditions (see Supplementary Table S1).

marine-edge settings, often the coasts of islands with fringing coral reefs. Seaward distance and geomorphic setting may influence C dynamics through differences in tidal flushing and relative importance of allochthonous (river sediment) versus autochthonous (*in situ* litter and root production) controls on soil C accumulation^{5,16}.

We found that mangroves are among the most C-dense forests in the tropics (sample-wide mean: 1,023 Mg C ha⁻¹ ± 88 s.e.m.), and exceptionally high compared to mean C storage of the world's major forest domains (Fig. 2). Estuarine sites contained a mean of 1,074 Mg C ha⁻¹ (±171 s.e.m.); oceanic sites contained 990 ± 96 Mg C ha⁻¹. Above-ground C pools were sizeable (mean 159 Mg C ha⁻¹, maximum 435 Mg C ha⁻¹), but below-ground storage in soils dominated, accounting for 71–98% and 49–90% of total storage in estuarine and oceanic sites, respectively (Figs 2 and 3). Below-ground C storage was positively but weakly correlated to above-ground storage ($R^2 = 0.21$ and 0.50 in estuarine and oceanic sites, respectively). Although soil C pools increased slightly with distance from the seaward edge in oceanic sites (because of increasing soil depth), changes in both above- and

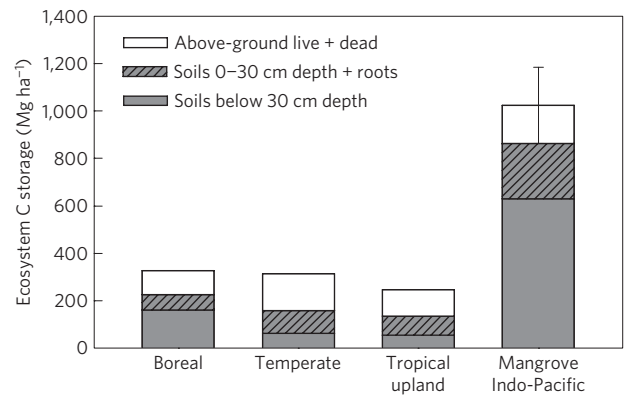


Figure 2 | Comparison of mangrove C storage (mean ± 95% confidence interval) with that of major global forest domains. Mean C storage by domain was derived from ref. 9, including default values for tree, litter, dead wood, root:shoot ratios, and soils, with the assumption that the top 30 cm of soil contains 50% of all C residing in soil⁹, except for boreal forests (25%). Domain means are presented for context; however some forest types within each contain substantially higher or lower C stores^{9,10}. In general, the top 30 cm of soil C are considered the most vulnerable to land-use change⁹; however in suboxic peat/muck soils, drainage, excavation, and oxidation may influence deeper layers²⁹.

below-ground C storage over this distance gradient were highly variable and not statistically significant (Fig. 3).

So far, quantification of below-ground C storage in mangroves has been impeded by a lack of concurrent data on soil carbon concentration, bulk density, and depth, and how these vary spatially^{5,21}. We found high C concentration (% dry mass) throughout the top metre of the soil profile, with a decrease below 1 m (Fig. 4a). Carbon concentration was lower in estuarine (mean = 7.9%) versus oceanic (mean = 14.6%) sites. Soil bulk density (BD) did not differ significantly by setting or distance from the seaward edge (generally ~0.35–0.55 g cm⁻³), but did increase with depth (Fig. 4b). Combining C concentration and BD yielded mean C densities of 0.038 g C cm⁻³ and 0.061 g C cm⁻³ in estuarine and oceanic soils, respectively. The total depth of the peat/muck layer differed between estuarine and oceanic sites (Fig. 4c) and was the main driver of variations in below-ground C storage (Fig. 3). Estuarine stands overlie deep alluvial sediment deposits, usually exceeding 3 m depth; oceanic stands contained a distinct organic-rich layer overlying hard coral sand or rock, with peat/muck thickness increasing from a mean of 1.2 m (±0.2 s.e.m.) near the seaward edge to 1.7 m (±0.2 s.e.m.) 135 m inland (Fig. 4c). In terms of total below-ground C storage, the shallower soil depth in oceanic mangroves was compensated in part by higher soil organic C concentration (Fig. 4a,c).

These data indicate that high productivity and C flux rates in mangroves^{16–22} are indeed accompanied by high C storage, especially below ground. High per-hectare C storage coupled with a pan-tropical distribution (total area ~14 million ha; refs 4,6) suggests mangroves are a globally important surface C reserve. Although our sample is not intended to represent all mangrove types (precluding simple scaling up), some constraints on global storage can be derived by combining an uncertainty range from our empirical data (5th to 95th percentile C storage values) with additional global data on soil C concentration, depth, and standing biomass^{16,17,21,23,24} (see Methods in Supplementary Information). This approach yields an estimate of 4.0–20 Pg C globally. This estimate will undoubtedly be refined, but suggests mangroves add significantly to tropical wetland forest C storage (for example, tropical peatlands: ~82–92 Pg C; ref. 12).

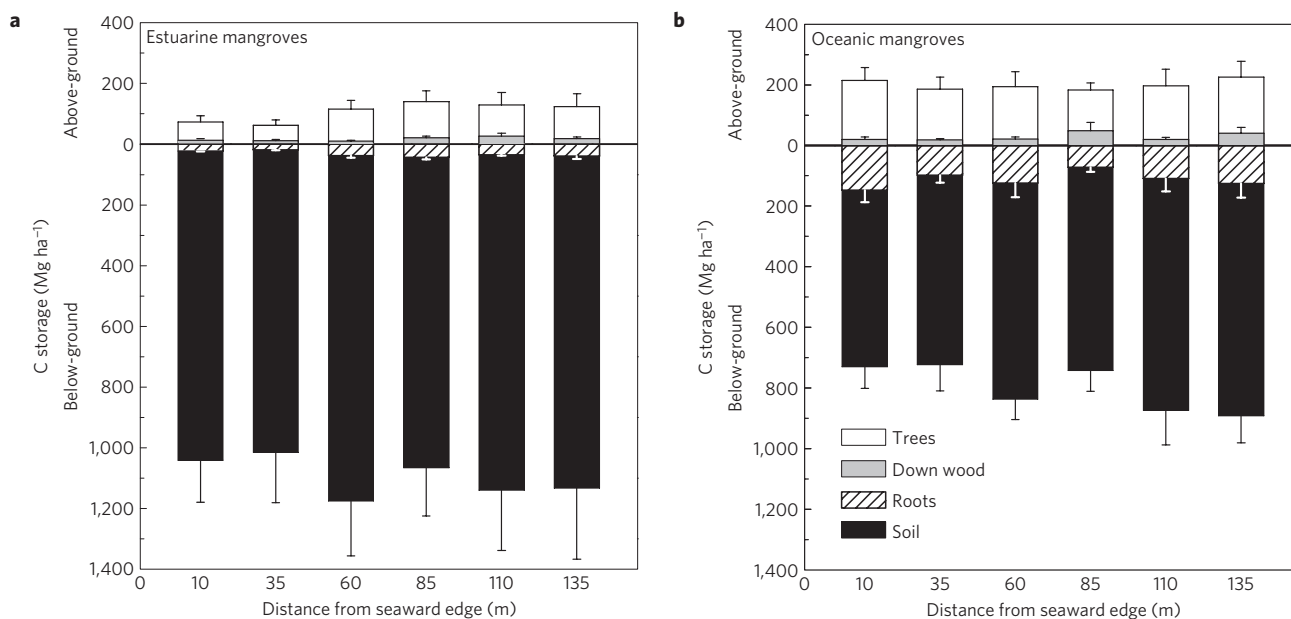


Figure 3 | Above- and below-ground C pools in Indo-Pacific mangroves, assessed by distance from the seaward edge. **a**, Estuarine mangroves situated on large alluvial deltas. **b**, Oceanic mangroves situated in marine edge environments—for example, island coasts. Below-ground C comprised 71–98% and 49–90% of ecosystem C in estuarine and oceanic sites, respectively. Overall carbon storage did not vary significantly with distance from the seaward edge in either setting over the range sampled ($P > 0.10$ for above-ground, below-ground, and total C storage by functional data analysis (FDA, see Methods); 95% CIs for rates-of-change all overlapped zero and were between -1.2 and 3.9 Mg C ha^{-1} per metre of distance from edge).

Carbon emissions from land-use change in mangroves are not well understood. Our data suggest a potential for large emissions owing to perturbation of large C stocks. The fate of below-ground pools is particularly understudied, but available evidence suggests that clearing, drainage, and/or conversion to aquaculture—aside from affecting vegetation biomass—also decreases mangrove soil C significantly^{16,22,26–28}. In upland forests, the top 30 cm of soil are generally considered the most susceptible to land-use change⁹; however in wetland forests, drainage and oxidation of formerly suboxic soils may also influence deeper layers²⁹. To provide some constraints on estimated emissions, we used a similar uncertainty propagation technique, combining our C storage values with other global data^{16,17} and applying a range of assumptions regarding land-use effects on above- and below-ground pools (see Supplementary Information). This approach yields a plausible estimate of 112–392 MgC released per hectare cleared, depending in large part on how deeply soil C is affected by different land uses. Coupled with published ranges of mangrove deforestation rate (1–2%; refs 1,4) and global area (13.7–15.2 million ha; refs 4,6), this estimate leads to global emissions on the order of 0.02–0.12 Pg C yr⁻¹. This rate adds significantly to oft-cited peatland emissions (0.30 Pg C yr⁻¹) and global deforestation emissions ($\sim 1.2 \text{ Pg C yr}^{-1}$; ref. 7) despite accounting only for loss of standing stocks but not other known mangrove-conversion influences, such as decreased C sequestration rate, burial efficiency, and export to ocean^{16,18}, nor increases in normally-low methanogenesis in some disturbed soils^{16,27}.

In addition to direct losses of forest cover, land-use activities will also impact mangrove responses to sea-level rise^{14,15}. Mangroves have been remarkably persistent through rapid sea-level rises (5–15 mm yr⁻¹) during the late Quaternary Period (0–18,000 yr BP) because of (1) landward migration, and (2) autogenic changes in soil-surface elevation through below-ground organic matter production and/or sedimentation¹⁵. Under current climate trends, sea level is projected to rise 18–79 cm from 1999–2099 (higher if ice-sheet melting continues accelerating)^{8,30}, implying a period-averaged rate of ~ 1.8 – 7.9 mm yr^{-1} , notwithstanding local varia-

tions and temporal nonlinearities. Although this rate is not unprecedented, it is unclear yet whether mangroves are currently keeping pace with sea levels^{14,15}. Anthropogenic influences could constrain future resilience to sea-level rise through coastal developments that impede inland migration (for example, roads, infrastructure), upland land uses that alter sediment and water inputs (for example, dams, land clearing), and mangrove degradation that reduces below-ground productivity¹⁴. This synergy of land use and climate change impacts presents additional uncertainties for the fate and management of coastal C stores.

Critical uncertainties remain before estimates of mangrove C storage and land-use emissions can be improved. Among these are geographic variations in soil depth, a key but unknown parameter in most regions^{3,21}. Similarly, empirical data on land-use change impacts on soil C is strongly lacking, especially for deep layers (but see refs 26–28). Quantitative estimates are also needed of the relative area occupied by estuarine/delta and oceanic/fringe mangroves, which is not addressed in most analyses of mangrove area^{4,6}. Because these two systems store below-ground C differently, improved spatial data will greatly refine estimates of global C storage and emissions owing to disturbance.

Our data show that discussion of the key role of tropical wetland forests in climate change could be broadened significantly to include mangroves. Southeast Asian peatlands are currently being advanced as an essential component of climate change mitigation strategies such as REDD+ (refs 7,13), and mangroves share many of the same relevant characteristics: deep organic-rich soils, exceptionally high C storage, and extensive deforestation/degradation resulting in potentially large greenhouse gas emissions. The well-known ecosystem services and geographic distribution of mangroves^{1–4} suggest these mitigation strategies could be effective in providing ancillary benefits as well as potential REDD+ opportunities in many tropical countries. Because land use in mangroves affects not only standing stocks but also ecosystem response to sea-level rise, maintaining these C stores will require both in situ mitigation (for example, reducing conversion rates) as well as facilitating adaptation to rising seas. The latter challenge is largely unique to management

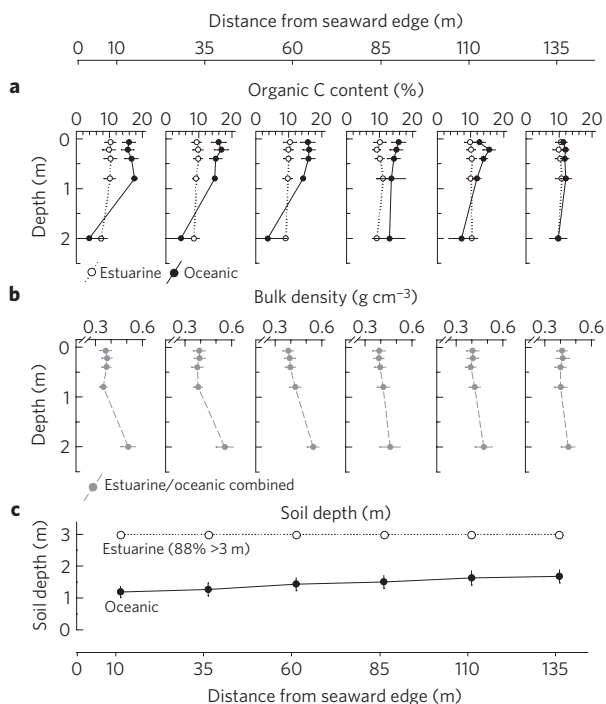


Figure 4 | Soil properties determining below-ground carbon storage in Indo-Pacific mangroves. **a**, Soil C concentration was greater in oceanic (mean = 14.6%) versus estuarine (mean = 7.9%) sites ($P = 0.001$), and decreased with depth ($P < 0.0001$; effect stronger in oceanic sites). Change in C concentration with seaward distance was biologically insignificant. **b**, Soil bulk density did not differ significantly with setting ($P = 0.79$); hence one line is shown combining both settings. Bulk density increased with depth ($P < 0.0001$) but not seaward distance ($P = 0.20$), and a distance \times depth interaction term was not significant ($P = 0.47$). **c**, Soil depth increased with distance from the seaward edge in oceanic stands (FDA result: $P = 0.002$, 95% CI for rate-of-change = 21–65 cm increase per 100 m distance).

of coastal forests, calling for watershed-scale approaches, such as landscape buffers for accommodating inland migration where possible, maintenance of critical upstream sediment inputs, and addressing degradation of mangrove productivity from pollution and other exogenous impacts^{14,15}.

Methods

We sampled 25 mangrove sites ($n = 10$ estuarine, $n = 15$ oceanic) across the Indo-Pacific (8°S – 22°N , 90° – 163°E) using a transect starting from, and running perpendicular to, the seaward edge. To maximize scope and representativeness, we stratified the sample across a broad range of stand conditions—including small-stature stands and shallow soils (<4 m canopy height, <10 cm mean tree diameter, <0.5 m soil depth) to large-stature stands and deep soils (>15 m canopy height, >20 cm mean tree diameter, soil depth >3 m) (Supplementary Table S1). These structural characteristics of forest stature and soil depth are primary determinants of C storage, probably more so than environmental gradients or geographic variation per se. Specific transect starts were determined randomly a priori from aerial imagery, notwithstanding constraints of access and land ownership. Within six circular sample plots spaced at 25-m intervals along each transect, we measured standing tree and down wood (dead wood on forest floor) biomass using standard biometric techniques (stem surveys, planar intercept transects), then applying region-specific or common allometric equations and C:biomass conversions for both above-ground and below-ground biomass. We measured soil depths at three systematic locations in each plot using a graduated aluminium probe (inference limit 3 m). We extracted a soil core from each plot using a 6.4-cm open-face peat auger to minimize sample disturbance/compaction, systematically divided the soil profile into depth intervals, and collected subsamples from each interval. Subsamples were dried to constant mass and weighed for bulk density determination, then analysed for C concentration using the dry combustion method (induction furnace). Standard error in total ecosystem C storage was computed by propagating standard errors of component pools. For

estuarine and oceanic sites separately, we analysed changes in soil depth and C pools with distance from the seaward edge using functional data analysis (site-level regressions for rate-of-change with distance, followed by a one-sample parametric test on all rates-of-change for strength of positive or negative relationship). We analysed spatial variations in soil C concentration and bulk density using linear mixed-effects regression models, assessing fixed effects of depth, distance from the seaward edge, and geomorphic setting, with a random effect of site to account for within-site dependence. Ranges for global C storage and emission rates were obtained using 5th percentile, mean, or 95th percentile estimates from this study (which accounts for the possibility that biomass and soil C pools differ globally from our mean values—higher or lower), with an adjusted soil C density based on a recent global analysis¹⁶, combined with recently published low to high estimates of global mangrove area and deforestation rate^{14,16}. See full Methods in Supplementary Information.

Received 30 September 2010; accepted 23 February 2011; published online 3 April 2011

References

- Duke, N. C. *et al.* A world without mangroves? *Science* **317**, 41–42 (2007).
- Polidoro, B. A. *et al.* The loss of species: Mangrove extinction risk and geographic areas of global concern. *PLoS ONE* **5**, e10095 (2010).
- Alongi, D. M. Present state and future of the world's mangrove forests. *Environ. Conserv.* **29**, 331–349 (2002).
- Food and Agriculture Organization of the United Nations (FAO). *The World's Mangroves 1980–2005* (FAO Forestry Paper 153. FAO, 2007).
- Bouillon, S., Rivera-Monroy, V. H., Twilley, R. R., Kairo, J. G. & Mangroves, in *The Management of Natural Coastal Carbon Sinks* (eds Laffoley, D. & Grimsditch) (IUCN, 2009).
- Giri, C. *et al.* Status and distribution of mangrove forests of the world using earth observation satellite data. *Glob. Ecol. Biogeogr.* **20**, 154–159 (2011).
- van der Werf, G. R. *et al.* CO₂ emissions from forest loss. *Nature Geosci.* **2**, 737–738 (2009).
- IPCC in *The Fourth Assessment Report Climate Change 2007* (eds Pachauri, R. K. & Reisinger, A.) (IPCC, 2007).
- Intergovernmental Panel on Climate Change (IPCC) in *Good Practice Guidance for Land use, Land-use Change, and Forestry* (eds Penman, J. *et al.*) (Institute for Global Environmental Strategies, 2003).
- Keith, H., Mackey, B. G. & Lindenmayer, D. B. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl Acad. Sci. USA* **106**, 11635–11640 (2009).
- Page, S. E. *et al.* The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature* **420**, 61–65 (2002).
- Page, S. E., Rieley, J. O. & Banks, C. J. Global and regional importance of the tropical peatland carbon pool. *Glob. Change Biol.* **17**, 798–818 (2011).
- Murdiyarso, D. M., Hergoualc'h, K. & Verchot, L. V. Opportunities for reducing greenhouse gas emissions in tropical peatlands. *Proc. Natl Acad. Sci. USA* **107**, 19655–19660 (2010).
- Gilman, E. L., Ellison, J., Duke, N. C. & Field, C. Threats to mangroves from climate change and adaptation options. *Aquat. Bot.* **89**, 237–250 (2008).
- Alongi, D. M. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuar. Coast Shelf Sci.* **76**, 1–13 (2008).
- Kristensen, E., Bouillon, S., Dittmar, T. & Marchand, C. Organic carbon dynamics in mangrove ecosystems. *Aquat. Bot.* **89**, 201–219 (2008).
- Komiyama, A., Ong, J. E. & Pongpan, S. Allometry, biomass, and productivity of mangrove forests. *Aquat. Bot.* **89**, 128–137 (2008).
- Twilley, R. R., Chen, R. H. & Hargis, T. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air Soil Pollut.* **64**, 265–288 (1992).
- Bouillon, S. *et al.* Mangrove production and carbon sinks: A revision of global budget estimates. *Glob. Biogeochem. Cycles* **22**, GB2013 (2008).
- Alongi, D. M. *et al.* Sediment accumulation and organic material flux in a managed mangrove ecosystem: Estimates of land–ocean–atmosphere exchange in peninsular Malaysia. *Mar. Geol.* **208**, 383–402 (2004).
- Chmura, G. L., Anisfeld, S. C., Cahoon, D. R. & Lynch, J. C. Global carbon sequestration in tidal, saline wetland soils. *Glob. Biogeochem. Cycles* **17**, 1111 (2003).
- Eong, O. J. Mangroves—a carbon source and sink. *Chemosphere* **27**, 1097–1107 (1993).
- Golley, F., Odum, H. T. & Wilson, R. F. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* **43**, 9–19 (1962).
- Fujimoto, K. *et al.* Belowground carbon storage of Micronesian mangrove forests. *Ecol. Res.* **14**, 409–413 (1999).
- Matsui, N. Estimated stocks of organic carbon in mangrove roots and sediments in Hinchinbrook Channel, Australia. *Mangr. Salt Marsh.* **2**, 199–204 (1998).
- Sjöling, S., Mohammed, S. M., Lyimo, T. J. & Kyaruzi, J. J. Benthic bacterial diversity and nutrient processes in mangroves: Impact of deforestation. *Estuar. Coast Shelf Sci.* **63**, 397–406 (2005).

27. Strangmann, A., Bashan, Y. & Giani, L. Methane in pristine and impaired mangrove soils and its possible effects on establishment of mangrove seedlings. *Biol. Fertil. Soils* **44**, 511–519 (2008).
28. Granek, E. & Ruttenberg, B. I. Changes in biotic and abiotic processes following mangrove clearing. *Estuar. Coast Shelf Sci.* **80**, 555–562 (2008).
29. Hooijer, A., Silvius, M., Wösten, H. & Page, S. PEAT-CO₂: *Assessment of CO₂ Emissions from Drained Peatlands in SE Asia*. Delft Hydraulics Report Q3943 (2006).
30. Church, J. A. *et al.* Understanding global sea levels: Past, present and future. *Sustain. Sci.* **3**, 9–22 (2008).

Acknowledgements

We thank our many international partners and field personnel for assistance with logistics and data collection: Kosrae Island Resource Management Authority; Yap State Forestry; Orangutan Foundation International; Indonesian Directorate General for Forest Protection and Nature Conservation; University of Manado and Bogor Agricultural University, Indonesia; Bangladesh Forest Department; and KPSKSA (Cilacap, Indonesia). We thank K. Gerow for statistical assistance, and R. Mackenzie,

C. Kryss and J. Bonham for assistance compiling site data. Funding was provided by USDA Forest Service International Programs and the Australian Agency for International Development (AusAID).

Author contributions

D.C.D. co-designed the study, collected field data, performed data analyses, and led the writing of the paper. J.B.K. conceived and co-designed the study, and contributed to data collection and writing. D.M. co-conceived the study, arranged for and contributed to data collection, and contributed to writing. S.K. contributed to data collection, data analysis, and writing. M.S. collected field data and contributed to writing. M.K. co-conceived the study and contributed to writing.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to D.C.D.