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Mangroves among the most carbon-rich forests in the tropics

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METHODS

Field sampling. In each of 25 sites distributed across the Indo-Pacific (8°S-22°N, 90°-163°E), we installed a sampling transect starting at, and running inland (perpendicular) from, the seaward edge. Sampling was conducted in 2008-2009. We stratified the sample across a broad range of stand conditions—comprising small-stature stands and shallow soils (<4 m canopy height or <10 cm mean tree diameter, <0.5 m soil depth) to large-stature stands and deep soils (>15 m canopy height or >20 cm mean tree diameter, soil >3 m) (Supplementary Table S1). These structural characteristics of forest stature and soil depth are primary determinants of C storage, likely more so than environmental gradients or geographic variation *per se*. Stratification ensured representation of a spectrum of stand types in addition to geographic breadth and estuarine versus oceanic settings (Supplementary Tables S1, S2). Specific transect starts were determined randomly *a priori* from aerial imagery, subject to constraints of access and land ownership. Six sampling plots were spaced at 25-m intervals along each transect, centered at 10, 35, 60, 85, 110, and 135 m from seaward edge; this transect distance allowed consistent sampling of both narrow and wide stands. (Note that Sundarbans plot arrangement differed due to need for consistency with local forest inventories, with four outer plots 50 m from central plot in cardinal directions, centered <150 m from watercourses; these sites were excluded from analyses involving distance from edge.) Estuarine mangroves (n=10) were situated on large alluvial deltas, often with a

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protected lagoon; oceanic mangroves (n=15) were situated in marine-edge environments, often the coasts of islands with fringing coral reefs. Sampled forests were dominated primarily by genera *Rhizophora*, *Bruguiera*, and/or *Sonneratia*, with lesser components of *Xylocarpus* and *Avicennia* (Sundarbans sites were dominated by *Heritiera* and *Excoecaria*) (Supplementary Table S1). Our scope of inference was defined as all above-ground C pools plus below-ground C to a maximum depth of 3 meters; therefore our C storage estimates are conservative in cases where organic soil depth exceeds 3 meters.

In each of the six plots per site, we measured all trees >5 cm stem diameter within a 7-meter radius, recording species, live/dead status, and stem diameter at 1.4 m height or 30 cm above highest buttress/prop-root (whichever higher)[31]. Saplings (<5 cm diameter) were similarly measured in a 2-meter radius. We measured down wood (dead wood lying on forest floor) volume using the planar intercept method[32] along four 12-meter subtransects emanating from each plot at 45° angles from the main transect. Understorey is generally negligible in mangroves[33] and was not sampled. We measured soil depths by inserting a graduated aluminium probe until refusal at subsurface bed layer (rock/coral) in three systematic locations near the center of each plot (probe length 3 m, inference limit of study). We extracted a soil core from the center of each plot with a 6.4-cm-diameter open-face peat auger, which minimized disturbance/compaction during the sampling process. The soil profile was systematically divided into depth intervals, consistent with one of the few published sources for Indo-Pacific mangrove soil profiles[34]: 0-15, 15-30, 30-50, and 50-100 cm, plus a deep horizon with variable interval depending on depth to underlying coral sand/rock. Subsamples of 76.7 cm^3 from each horizon were collected and dried immediately at 60 °C to constant mass.

Sample and Data Analysis. We computed above- and below-ground tree biomass for each measured individual using published mangrove allometric equations and wood densities specific to the region[17,35,36]. Down wood volume was converted to biomass using region-, size-class-, and decay-class-specific wood density determined via collections made during the study[32]. Tree and down wood biomass values were converted to C mass using a locally derived, conservative C:biomass ratio of 0.464 (ref. 35). To determine soil C storage, dried soil samples were weighed for bulk density determination, then ground, homogenized, passed through a 2-mm sieve, and analyzed for C concentration using the combustion method[37,38]. Inorganic (carbonate) C is generally negligible in Indo-Pacific mangrove sediments[20] and was not analyzed separately; however dilute acid treatment for carbonate removal was applied to samples from sites with significant fraction of coral fragments, etc.[37,38]. We also determined that soil bulk density estimates obtained via drying at 60 °C are within ~1% of those obtained via drying at 105 °C. Bulk density and carbon concentration were then combined with plot-specific soil depth measurements to obtain per-area soil C. Ecosystem C storage was computed as the sum of all tree, root, wood, and soil components; standard error of the total was obtained by propagating standard errors of component pools[39].

We used functional data analysis (FDA) to analyze changes in soil depth and C pools with distance from seaward edge. In this study context, FDA entailed assessing the rate of change-with-distance within each site using linear regression, followed by a parametric *t*-test of the degree to which the total sample of change-rates differed from zero. Tests were performed separately for estuarine and oceanic sites. We analyzed spatial variations in soil C concentration and bulk density using linear mixed-effects regression models, assessing the effect of depth, distance from seaward edge, and geomorphic setting (estuarine vs. oceanic). Mixed-effects

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models flexibly represent the covariance structure due to grouping of data (in this case, plots within site) by associating random effects to observations sharing the same level of a classification factor[40]. Thus the analysis was performed at the plot level with site as a random term to account for within-site dependencies; parameters were estimated by restricted maximum likelihood. Interaction terms were included in models, and data were $\log_e$-transformed where necessary to meet assumptions of constant variance and normality.

Global estimates. Estimating global C storage and land-use emissions in mangroves is a useful exercise, but is made difficult by a paucity of data on below-ground C storage in most regions (i.e., combined data on C concentration, bulk density, and depth), as well as land-use change effects on C pools. Data from this study can be used to inform these estimates, while taking into account that, although broad, the sample is not a comprehensive global sample representing all mangroves. We addressed this issue by employing two complementary approaches: uncertainty propagation and adjustments based on other global data sets.

For the uncertainty propagation, we first scaled up to global C storage using data from the extreme low end (5^{th}-percentile) of our distribution—e.g., low biomass, shallow soil, and thus low C storage—in effect assuming that mangroves worldwide are, on average, at the small-stature end of the range we observed. We repeated the calculation using data from the extreme high end (95^{th}-percentile) of our distribution—e.g., high biomass, deep soil, and thus high C storage—in effect assuming that mangroves worldwide are, on average, at the large-stature end of our range. Fifth and 95^{th} percentiles were used to avoid influence of outliers in either direction. Individually, both of these extremes may be improbable, but taken together are likely to contain the true global per-hectare C store, even if our sample differs from the global mangrove population. We propagated this uncertainty by combining the low-end estimate with a published low estimate of global mangrove area (13.8 million ha)[6], then combining the high-end estimate with a published high estimate of global mangrove area (15.2 million ha)[4]. Finally, we applied an adjustment factor to our soil C density based on the most comprehensive global dataset available on mangrove soil C concentration (%OC by mass)[16]. Those data show a median C concentration of 2.2% in mangroves, which, when combined with the well-known inverse relationship between C concentration and BD (e.g., using data from this study yielded the quantitative relationship [$\%OC=3.0443*BD^{-1.313}$], R^2=0.62, Supplementary Figure S1) suggests a representative soil C density of ~0.028 g C cm^{-3}. This value is ~35% lower than we observed for the Indo-Pacific region (0.043 g C cm^{-3} when averaged by region). Therefore, in calculating the uncertainty range described above, we multiplied our soil C values by an adjustment factor of (1-0.35) to yield more conservative estimates of global C storage. (Final values for global scaling exercise: 5th-percentile: 32.6 Mg C ha^{-1} biomass and 256 Mg C ha^{-1} soil, final 95th-percentile: 501 Mg C ha^{-1} biomass and 813 Mg C ha^{-1} soil). Note that these adjustments were only applied for global scaling exercises, not to any regional results presented in Figures 2-4, which have direct inference to the Indo-Pacific region.

Estimating global emissions from land-use change was conducted using a similar uncertainty-propagation approach, applying a range of simple but plausible assumptions regarding the fate of various C pools with mangrove conversion. We again combined our C pool estimates with those from global compilations[16,17], then, for the low-end estimate of conversion impact, applied 50% biomass loss, 25% loss of soil C from the top 30 cm, and no loss from deeper layers. For the high-end estimate of conversion impact, we applied 100% biomass loss, 75% loss of soil C from the top 30 cm, and 35% loss from deeper layers. The lower end may apply to land uses that

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degrade mangroves such as overharvest and/or moderate soil disturbance, while the upper end may apply to heavier activities such as shrimp aquaculture which can involve complete forest clearing and excavating/piling of the top 50-100+ cm of soil. This yields a plausible estimate of 112-392 Mg C released per hectare affected. We then combined this range with published ranges of mangrove area (13.8-15.2 million ha)[4,6] and deforestation rate (1-2% yr^{-1})[1,4], propagating low-end estimates to obtain the low extreme and high-end estimates to obtain the high extreme. We used a range of mangrove area values because the most recent source is likely a conservative estimate of total area[6], and because recent emission rates come not just from current area but from that affected by deforestation over the past decades—by definition a greater area[4].

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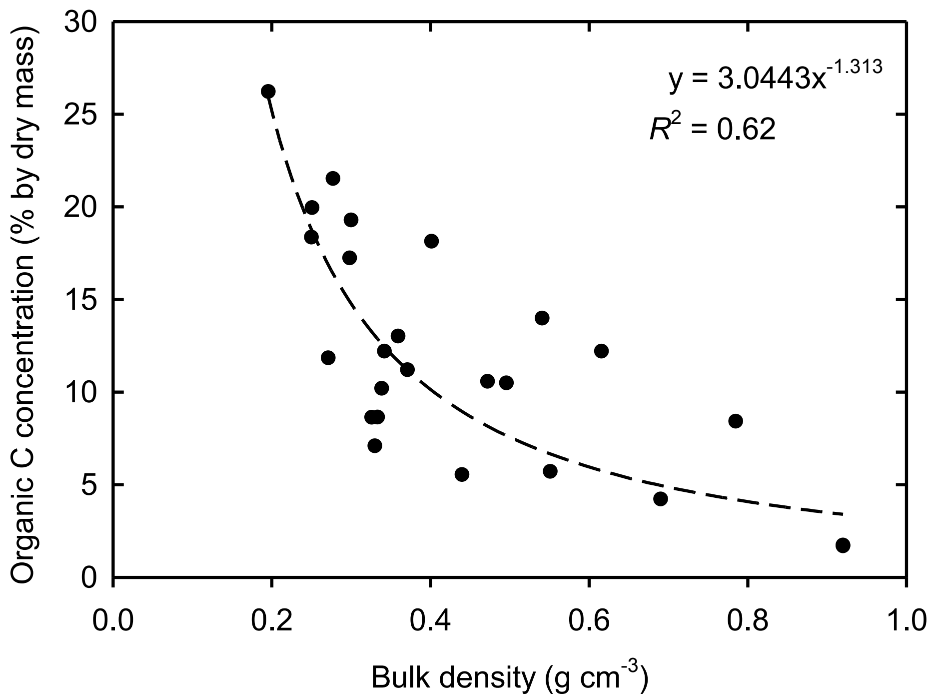

Supplementary Figure S1. Relationship between organic carbon concentration and bulk density of mangrove soils from the 25 sample stands across the Indo-Pacific region.

Supplementary Table S1. General characteristics of sampled mangrove forests, parsed by stature class*.

Small-stature (n=9)						Intermediate-stature (n=5)						Large-stature (n=11)					
Site †	Geo-morphic setting ‡	Latitude, Longitude (degrees)	Forest size (ha)	Tidal range (m) ¥	Cover type §	Site †	Geo-morphic setting ‡	Latitude, Longitude (degrees)	Forest size (ha)	Tidal range (m) ¥	Cover type §	Site †	Geo-morphic setting ‡	Latitude, Longitude (degrees)	Forest size (ha)	Tidal range (m) ¥	Cover type §
Y1	Ocean.	9.55631 N 138.17981 E	10	1.5	S/R	Y2	Ocean.	9.51450 N 138.14933 E	70	1.5	S/R	K1	Ocean.	5.34919 N 162.96306 E	60	1.7	S
G1	Estuar.	22.25585 N 89.62956 E	10^6	--	H/E	S5	Ocean.	1.29617 N 124.50681 E	80	2.5	S/R	K2	Ocean.	5.28219 N 162.96406 E	70	1.7	S/B
J1	Estuar.	7.71289 S 108.95828 E	500	1.2	S/R	S6	Estuar.	1.37225 N 124.55069 E	120	2.5	R	K3	Ocean.	5.32633 N 162.94497 E	90	1.7	S/B
J2	Estuar.	7.72369 S 108.97044 E	2700	1.2	S/R	G2	Estuar.	22.31942 N 89.62878 E	10^6	--	H/E	K4	Ocean.	5.28328 N 162.91050 E	25	1.7	S/R
S1	Ocean.	1.74986 N 124.73622 E	220	2.5	R	B1	Estuar.	2.73667 S 111.73775 E	500	3.0	R/B	Y3	Ocean.	9.55278 N 138.09983 E	15	1.5	S/B
S2	Ocean.	1.69453 N 124.95869 E	70	2.5	R/X							Y4	Ocean.	9.54253 N 138.09072 E	15	1.5	S/B
S3	Ocean.	1.73781 N 124.75486 E	150	2.5	R							Y5	Ocean.	9.58842 N 138.12747 E	20	1.5	S/B
S4	Ocean.	1.56733 N 124.80381 E	35	2.5	S/R							B2	Estuar.	2.84886 S 111.73872 E	125	3.0	B/R
P1	Ocean.	7.35211 N 134.53911 E	40	1.9	R							B3	Estuar.	2.78389 S 111.69878 E	150	3.0	R
												B4	Estuar.	2.85594 S 111.73181 E	65	3.0	B/R
												B5	Estuar.	2.74128 S 111.71383 E	175	3.0	R

* Stature classes are defined as: Small, <10 cm mean tree diameter or <4 m canopy height; Intermediate 10-20 cm mean tree diameter and 4-15 m canopy height; Large, >20 cm mean tree diameter or >15 m canopy height.

† Sites: B, Borneo; G, Ganges-Brahmaputra Delta (Sundarbans, Bangladesh); J, Java; K, Kosrae; P, Palau; S, Sulawesi; Y, Yap.

‡ Geomorphic settings: Estuar., estuarine/river-delta site; Ocean., oceanic/fringe site.

¥ Tidal ranges are region-scale values determined from minimum/maximum tide levels during 2010. Values are not listed for Ganges-Brahmaputra Delta sites due to dominance by seasonal (monsoonal) river flooding regimes rather than well-quantified tidal ranges.

§ Cover type defined by tree genus dominance by basal-area: B, *Bruguiera*; E, *Excoecaria*; H, *Heritiera*; R, *Rhizophora*; S, *Sonneratia*; X, *Xylocarpus*.

9

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Supplementary Table S2. Carbon pool data for each sampled stand.

Site*	Geomorphic setting	Total ecosystem C	Total above-ground C	Total below-ground C	Tree C (stem, branch, foliage)	Tree C (roots)	Down wood C	Soil C	Soil depth (cm)	Soil bulk density (g cm^{-3})	Soil % OC
G1	Estuarine	547.0	107.4	439.6	103.3	53.6	4.2	386.0	300	0.920	1.69
G2	Estuarine	584.1	60.0	524.1	56.1	32.3	3.9	491.8	300	0.920	1.74
J1	Estuarine	437.0	6.5	430.5	2.3	0.5	4.2	430.0	142	0.551	5.71
J2	Estuarine	736.4	17.1	719.4	12.7	6.2	4.3	713.2	281	0.440	5.54
B1	Estuarine	1044.2	78.3	965.9	67.1	22.4	11.2	943.5	300	0.326	8.63
B2	Estuarine	1472.0	181.7	1290.3	145.1	55.8	36.7	1234.5	300	0.336	8.65
B3	Estuarine	1307.5	196.6	1110.9	178.7	61.9	17.9	1049.0	300	0.339	10.1
B4	Estuarine	1391.7	103.9	1287.8	84.8	32.8	19.0	1255.0	300	0.271	11.8
B5	Estuarine	1016.2	154.8	861.5	145.8	47.6	9.0	813.9	300	0.330	7.09
S6	Estuarine	2202.9	111.0	2091.8	89.1	28.2	21.9	2063.6	300	0.401	18.1
S1	Oceanic	734.0	145.8	588.2	93.2	27.5	52.6	560.7	81	0.785	8.42
S2	Oceanic	415.1	115.0	300.0	29.8	9.8	85.3	290.2	48	0.277	21.5
S3	Oceanic	774.6	68.0	706.6	44.0	10.5	24.0	696.0	122	0.300	19.3
S4	Oceanic	859.3	87.4	772.0	55.4	31.5	32.0	740.4	103	0.541	14.0
S5	Oceanic	716.0	97.7	618.2	56.7	36.9	41.1	581.3	80	0.616	12.2
P1	Oceanic	706.5	118.1	588.4	104.4	67.8	13.8	520.6	117	0.250	18.4
Y1	Oceanic	823.2	140.0	683.2	132.2	80.4	7.8	602.8	144	0.342	12.2
Y2	Oceanic	895.8	205.3	690.5	186.7	107.8	18.6	582.7	124	0.251	20.0
Y3	Oceanic	1345.7	280.5	1065.2	268.2	190.3	12.3	874.9	174	0.298	17.2
Y4	Oceanic	1046.4	246.5	799.9	238.5	168.3	8.0	631.6	144	0.371	11.2
Y5	Oceanic	1775.4	434.8	1340.7	418.5	263.1	16.3	1077.6	223	0.496	10.5
K1	Oceanic	870.6	247.2	623.4	237.9	195.9	14.0	427.5	74	0.359	13.0
K2	Oceanic	1676.0	250.1	1425.9	242.5	203.7	7.6	1222.3	275	0.472	10.6
K3	Oceanic	1172.4	303.1	869.3	248.1	194.0	55.1	675.3	299	0.690	4.23
K4	Oceanic	1032.8	223.8	809.0	193.0	86.7	30.8	722.3	155	0.196	26.2
Estuarine mean		1073.9	101.7	972.2	88.5	34.1	13.2	938.1	282.3	0.483	7.9
Oceanic mean		989.6	197.6	792.0	169.9	111.6	28.0	680.4	144.2	0.416	14.6
Grand mean		1023.3	159.2	864.1	137.4	80.6	22.1	783.5	199.4	0.443	11.9

All data are in Mg C ha^{-1} except where noted otherwise.

*Sites: B, Borneo; G, Ganges-Brahmaputra Delta (Sundarbans, Bangladesh); J, Java; K, Kosrae; P, Palau; S, Sulawesi; Y, Yap.