




Mangrove blue carbon stocks and dynamics are controlled by hydrogeomorphic settings and land-use change

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Abstract

Globally, carbon-rich mangrove forests are deforested and degraded due to land-use and land-cover change (LULCC). The impact of mangrove deforestation on carbon emissions has been reported on a global scale; however, uncertainty remains at sub-national scales due to geographical variability and field data limitations. We present an assessment of blue carbon storage at five mangrove sites across West Papua Province, Indonesia, a region that supports 10% of the world's mangrove area. The

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sites are representative of contrasting hydrogeomorphic settings and also capture change over a 25-years LULCC chronosequence. Field-based assessments were conducted across 255 plots covering undisturbed and LULCC-affected mangroves (0-, 5-, 10-, 15- and 25-year-old post-harvest or regenerating forests as well as 15-year-old aquaculture ponds). Undisturbed mangroves stored total ecosystem carbon stocks of 182–2,730 (mean \pm SD: 1,087 \pm 584) Mg C/ha, with the large variation driven by hydrogeomorphic settings. The highest carbon stocks were found in estuarine interior (EI) mangroves, followed by open coast interior, open coast fringe and EI forests. Forest harvesting did not significantly affect soil carbon stocks, despite an elevated dead wood density relative to undisturbed forests, but it did remove nearly all live biomass. Aquaculture conversion removed 60% of soil carbon stock and 85% of live biomass carbon stock, relative to reference sites. By contrast, mangroves left to regenerate for more than 25 years reached the same level of biomass carbon compared to undisturbed forests, with annual biomass accumulation rates of 3.6 \pm 1.1 Mg C ha⁻¹ year⁻¹. This study shows that hydrogeomorphic setting controls natural dynamics of mangrove blue carbon stocks, while long-term land-use changes affect carbon loss and gain to a substantial degree. Therefore, current land-based climate policies must incorporate landscape and land-use characteristics, and their related carbon management consequences, for more effective emissions reduction targets and restoration outcomes.

KEYWORDS

climate change mitigation, coastal wetlands, Indonesia, LULCC, Paris Agreement, restoration

1 | INTRODUCTION

Mangrove forests are one of the most productive and efficient long-term natural carbon sinks (Bouillon et al., 2008; Donato et al., 2011), and as such have been identified alongside seagrasses and salt-marshes as key 'blue carbon' ecosystems (Lovelock & Duarte, 2019). Mangroves have experienced large-scale deforestation and conversion to other land uses, particularly in Southeast Asia (Hamilton & Casey, 2016; Richards & Friess, 2016). Mangrove deforestation and conversion generates substantial carbon emissions (Atwood et al., 2017; Hamilton & Friess, 2018), accounting for a substantial proportion of greenhouse gas (GHG) emissions for some countries (Murdiyarso et al., 2015; Taillardat, Friess, & Lupascu, 2018).

Recently, the conservation of mangrove carbon stocks has been promoted in global climate negotiations due to their potential contribution to mitigating GHG emissions. In response, the number of mangrove blue carbon assessments has increased rapidly over the past decade (Adame et al., 2013; Donato et al., 2011; Kauffman, Heider, Norfolk, & Payton, 2014; Nam, Sasmito, Murdiyarso, Purbopuspito, & MacKenzie, 2016; Stringer, Trettin, Zarnoch, & Tang, 2015; among many others). However, the majority of mangrove carbon studies have been conducted in natural or relatively undisturbed systems, making it difficult to generate estimates of carbon stock loss or

recovery as a consequence of land-use change and restoration efforts (Sasmito, Taillardat, et al., 2019). Estimates of carbon stock loss are further complicated by the fact that biomass and soil carbon vary substantially across climatic gradients (Simard et al., 2019) and geomorphological settings (Rovai et al., 2018; Twilley, Rovai, & Riul, 2018).

This study investigates the variation in mangrove carbon stocks across hydrogeomorphic settings, as well as their loss and recovery following land-use change in West Papua Province, Indonesia. We first assessed and compared total carbon stocks and other biophysical factors (i.e., forest structure and physicochemical soil properties) in undisturbed mangroves across different hydrogeomorphic settings. Second, we compared and identified the changes in carbon stocks between undisturbed mangrove forests and forests affected by land-use change (i.e., mangrove harvesting, regeneration and aquaculture) across a 25-year chronosequence. Third, we calculated potential carbon stock loss and recovery resulting from these new land management practices. Our findings contribute to an enhanced understanding of current blue carbon stocks as well as the potential emissions and removals generated by mangrove management in an important region of the global mangrove cover, and can therefore be used to refine national carbon emissions calculations.

2 | MATERIALS AND METHODS

2.1 | Hydrogeomorphic settings and land use in sampling sites

The study was conducted in the Bintuni and Kaimana Regencies of West Papua Province, Indonesia. The Papua region, encompassing the provinces of West Papua and Papua, represents nearly 10% of global mangrove forest area (Hamilton & Casey, 2016), and Bintuni Bay in particular has been identified as a global hotspot for mangrove biomass (Simard et al., 2019). Generally, mangrove forests in Bintuni Bay are identified as a tidal estuarine hydrogeomorphic setting, with undisturbed mangrove stands reaching up to 30 m in height (Sillanpää, Vantellingen, & Friess, 2017; Simard et al., 2019). Nearly, 30 true mangrove tree species have been recorded in Bintuni Bay (Kusmana & Onrizal, 2003).

Field sampling was carried out across five study sites (Table 1; Figure 1), which were divided into distinct hydrogeomorphic settings according to a macro-scale hydrogeomorphic typology developed by Worthington and Spalding (2018) and overlaid with our sampling locations. The sampling sites were located in two mangrove hydrogeomorphic settings: estuarine and open coast (Figure 1). To understand spatial variation in biophysical and hydrological properties within the macro-scale typological units, a meso-scale typology, fringe and interior mangroves, was nested within the macro-scale typology. The meso-scale classifications were determined by distinct hydrodynamics and sediment

supply characteristics between fringe and interior mangrove locations (Woodroffe et al., 2016). Subsequently, we compared carbon stocks, forest structure and soil properties of undisturbed

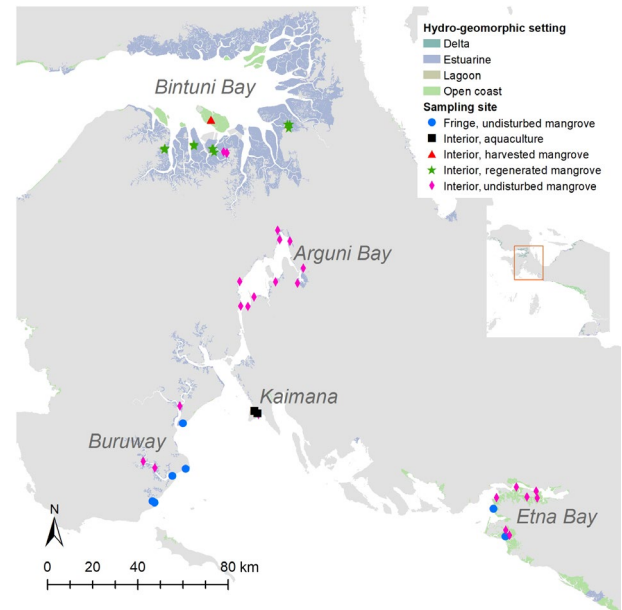


FIGURE 1 Location of carbon sampling sites in West Papua Province, Indonesia. The range of hydrogeomorphic settings is indicated in different colors, while sites with different proximity to open water and different management regimes are indicated by closed shapes of different colors

TABLE 1 Summary of mangrove settings, land-use types, year of field sampling and number of sampled plots across study sites

Site	Macro-scale setting (hydrogeomorphic variation)	Meso-scale setting (hydrodynamic or tidal elevation)	Land-use description	Sampling year	Number of plots	Soil depth (cm)	Dominant species
Arguni Bay	Estuarine	Interior	Undisturbed forest	2015	41	300	<i>Rhizophora</i> spp. (41%)
Bintuni Bay	Estuarine	Interior	Undisturbed forest	2018	18	300	<i>Rhizophora apiculata</i> (33%)
	Open coast	Interior	Harvested forest	2018	18	300	—
	Estuarine	Interior	Post-harvest forest (5-year old)	2018	18	300	<i>R. apiculata</i> (44%)
	Estuarine	Interior	Post-harvest forest (10-year old)	2018	18	286	<i>R. apiculata</i> (91%)
	Estuarine	Interior	Post-harvest forest (15-year old)	2018	18	300	<i>R. apiculata</i> (88%)
Estuarine	Interior	Post-harvest forest (25-year old)	2018	18	300	<i>R. apiculata</i> (81%)	
Buruway	Estuarine	Interior	Undisturbed forest	2017	17	230	<i>R. apiculata</i> (37%)
	Estuarine	Fringe	Undisturbed forest	2017	28	107	<i>R. apiculata</i> (36%)
Etna	Open coast	Interior	Undisturbed forest	2017	43	234	<i>R. apiculata</i> (47%)
	Open coast	Fringe	Undisturbed forest	2017	6	190	<i>R. apiculata</i> (50%)
Kaimana	Estuarine	Interior	Undisturbed forest	2017	5	113	<i>Rhizophora mucronata</i> (39%)
	Estuarine	Interior	Aquaculture (15-year old)	2017	7	56	<i>R. apiculata</i> (49%)
Total					255		

mangrove across four hydrogeomorphic mangrove settings: estuarine fringe (EF), estuarine interior (EI), open coast fringe and open coast interior mangroves (see Table 1 for detailed descriptions of the sampling locations).

Undisturbed mangroves were located across all sampling sites (Table 1) and characterized by limited anthropogenic disturbance. In addition, three different land-use types, namely harvested mangrove, post-harvest or regenerating mangroves and aquaculture ponds at two sites (Bintuni Bay and Kaimana), were sampled for carbon stocks. In the post-harvest mangrove site in Bintuni Bay, mangrove stands were rotationally harvested for sustainable forestry products that more than 25 years old (Sillanpää et al., 2017). Forest stands at post-harvest mangrove sites were logged within the same year as we carried out our carbon stock field survey. Moreover, we assessed carbon stocks across different regenerating mangrove stands or rotational harvesting ages (5, 10, 15 and 25 years). We also performed a further carbon stock assessment within an aquaculture development in Kaimana, which was established in a former mangrove forest 15 years prior to our survey.

2.2 | Field sampling and data analyses

2.2.1 | Sampling design

We established 255 circular plots (each with an area of 314 m², covering a total area of 8 ha) along 48 transects across the five study sites. The plots were distributed across four mangrove hydrogeomorphic settings (described in Table 1), with field assessments conducted between 2015 and 2018. Total ecosystem carbon stocks were assessed for four carbon stock pools: above-ground tree biomass carbon (AGBC), dead wood carbon, below-ground root biomass carbon (BGBC) and soil carbon. The sampling plot size and design were adapted from a globally applied protocol for mangrove ecosystem carbon stock assessment (Kauffman & Donato, 2012). A maximum of six circular plots were established along each transect perpendicular to the coastline or tidal creek. At each plot, we measured tree diameter, counted and measured dead wood diameter, as well as collected dead wood and soil samples.

2.2.2 | Forest structure and biomass carbon stocks assessment

We measured tree diameter at breast height (DBH), which was generally considered 130 cm above the forest floor or 30 cm above the highest prop root for *Rhizophora* spp. (Kauffman & Donato, 2012). DBH was measured inside two different plots determined by DBH classes: circular plots of 10 m radius for trees with DBH > 5 cm and circular, nested plots of 2 m radius for mangrove saplings and seedlings with DBH < 5 cm. Standing dead tree status was documented following the dead tree definition of Kauffman and Donato (2012), and carbon stock correction factors were applied accordingly.

Tree and root biomasses were estimated from tree DBH data using species-specific allometric equations (Table S1). Biomass was estimated using standard carbon content factors of 47% and 39% for above-ground and below-ground biomass, respectively, as described by Kauffman and Donato (2012), and was expressed as carbon stocks in Mg C/ha. We calculated stand basal area (m²/ha) by summing basal area (m²) for all trees across the surveyed area and dividing with plot area (ha). We estimated tree density (trees/ha) by counting tree quantities (trees) across the surveyed area and dividing by area (ha).

2.2.3 | Dead wood carbon pool

We measured all dead, downed wood, including stem, branch and prop root debris lying on the forest floor, using the planar intercept technique described by Kauffman and Donato (2012). We classified dead wood into four classes based on its diameter (*D*): fine ($D < 0.6$ cm), small ($0.6 \text{ cm} < D < 2.5$ cm), medium ($2.5 \text{ cm} < D < 7.5$ cm) and large sound or rotten class ($D > 7.5$ cm). Two diagonal line transects were established and intersected in the midpoint of each circular plot. The DBH for large sound and rotten woody debris classes were measured, while all fine, small and medium classes were only recorded. Specific gravity of all woody debris classes was measured using the water displacement method, while carbon content was obtained from carbon and nitrogen (CN) elemental analysis. Means of quadratic mean diameter (cm), specific gravity (g/cm³) and carbon content (%) of the samples from our study are summarized in Table S2. Woody debris carbon stocks of all classes were averaged from all diagonal line transects within the plot.

2.2.4 | Soil carbon pool

We collected soil samples from the center of each circular plot using a stainless steel Eijkelkamp peat soil auger. A 5 cm sample of sediment was extracted from the midpoint of fixed horizons at depths of 0–15, 15–30, 30–50, 50–100 and >100 cm along the core. Organic soil depths varied depending on hydrogeomorphic setting and degree of degradation. Specifically, in Bintuni Bay where estuarine mangroves occurred, typically with a deep soil organic matter layer, we extended soil sample collection up to 300 cm, and samples were extracted from the midpoint of 100–200 cm, and from the deepest layer. In total, we collected 1,068 soil samples from all study sites.

Soil samples were processed by oven drying at 60°C until constant weight was reached. Bulk density (g/cm³) was determined for each sample by dividing the dried weight (g) with the given soil auger volume (cm³). Samples were ground using a mortar and pestle and passed through a 0.5 mm sieve to remove large roots and inorganic debris. A CN elemental analysis was used to obtain carbon content of soil samples from Bintuni Bay, whereas a loss on ignition (LOI) approach was applied for samples collected from Arguni Bay, Buruway,

Etna Bay and Kaimana. Consequently, we corrected the carbon content of one-third of LOI-derived soil organic matter samples using CN elemental analysis data, and the correction factors were applied to the rest of LOI-derived soil organic matter. An inorganic carbon content correction was conducted using the CN elemental analysis approach (Howard, Hoyt, Isensee, Pidgeon, & Telszewski, 2014) and applied to one-fifth of total samples. Soil carbon stock (Mg C/ha) was the final product of bulk density (g/cm^3) multiplied with the corrected carbon content (%) scaled by depth intervals (cm). Carbon density ($\text{mg C}/\text{cm}^3$) was calculated using data on bulk density and carbon content.

2.2.5 | Carbon stock loss and recovery calculation

We applied a Shapiro–Wilk normality and Levene's homogeneity test prior to statistical comparisons, with a logarithmic and square root transformation applied if data were not normally distributed and failed the homogeneity test. When the data were normally distributed, we used a one-way analysis of variance and Bonferroni multiple comparison test to compare carbon stocks, forest structure and soil properties between sampling plots and land-use and land-cover change types. We applied a nonparametric Kruskal–Wallis and Wilcoxon rank sum multiple comparison test for datasets that were not distributed normally and homogeneously. When carbon stocks at each pool were statistically different ($p < .05$), a carbon stocks difference approach was applied to estimate carbon stock loss and recovery impacted by land uses.

Carbon stock loss and recovery were estimated by subtraction of carbon stock pools between undisturbed reference mangrove forest and land-use affected sites (Arifanti, Kauffman, Hadriyanto, Murdiyarto, & Diana, 2019; Kauffman et al., 2017, 2018). The reference forest was the one closest to each land-use type, within the same study site. Reference forests for rotational harvesting and regeneration land-use types were in Bintuni Bay. In addition, reference forest for aquaculture was chosen from Kaimana. For the soil carbon pool assessment, we standardized soil carbon stocks using the soil mass equivalent approach modified from Ellert, Janzen,

Vandenbygaert, and Bremer (2007). The minimum soil mass value at Bintuni and Kaimana, respectively, was used to standardize soil carbon stocks for each soil layer. This standardization allowed the reduction of uncertainty sourced from soil compaction impacted by land-use change.

To determine the best variables to predict total ecosystem carbon stocks, we used simple and multiple generalized linear regression models (R function 'glm') and applied at a plot level dataset (sensu Paz et al., 2016). We first defined a priori variables which may control total ecosystem carbon stocks, namely hydrogeomorphic setting, land-use change, basal area, tree density, number of tree species, bulk density, carbon content, carbon density and soil depth. We used the R function 'dredge' to select the best regression models based on their AICc (corrected Akaike information criterion). The best fit models that were considered in the results were models with $\Delta\text{AICc} < 4$. All raw data from this study are accessible through the CIFOR Dataverse digital repository (Sasmito et al., 2019a, 2019b, 2019c), and all R code used for statistical analysis can be found in the online GitHub repository (<https://github.com/ssasmito/Papua-mangrove-blue-carbon>).

3 | RESULTS

3.1 | Carbon stock variation across undisturbed mangroves

Total carbon stocks of undisturbed mangroves in Papua ranged between 182 and 2,730 (mean \pm SD here after: $1,087 \pm 584$) Mg C/ha (Figure 2a). Total carbon stocks were significantly different among sites ($p < .05$; Figure 2a) and hydrogeomorphic settings ($p < .05$; Figure 2b). Across sampling sites, the largest mean of total carbon stocks was obtained at Arguni Bay ($1,686 \pm 564$ Mg C/ha), while the lowest was found at Kaimana (645 ± 418 Mg C/ha). In relation to the coastal hydrogeomorphic setting (Figure 2b), El mangroves stored the largest total carbon stocks ($1,480 \pm 552$ Mg C/ha). By contrast, EF mangrove settings stored the lowest total carbon stocks, with 432 ± 193 Mg C/ha or only one-third of the carbon stocks found

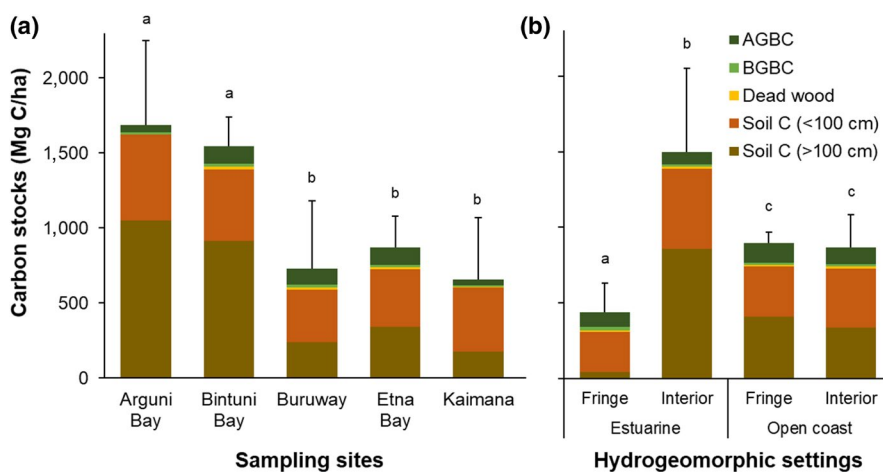


FIGURE 2 Variation of carbon stocks across carbon pools and undisturbed mangroves, showing (a) sampling sites and (b) hydrogeomorphic settings. Letters above boxplot bars denote significant difference between sites and coastal hydrogeomorphic settings resulting from multiple comparison analysis ($p < .05$). Error bars represent standard deviation of total carbon stocks

in EI settings. In open coast mangroves, total carbon stocks between fringe and interior settings were similar, at 865 ± 72 and 867 ± 216 Mg C/ha ($p > .05$).

Between carbon pools, 89% of total carbon stocks were stored in the soil, while 10% and 1% were in biomass and dead wood, respectively. Both the total soil carbon stocks and stocks in the top 100 cm differed significantly among sites and hydrogeomorphic settings ($p < .05$; Figure 2a,b; Table S3). Total soil carbon stocks in Arguni and Bintuni Bay (EI mangroves) were twice as large as stock estimates at Buruway, Etna Bay and Kaimana (open coast and EF mangroves). This pattern was associated with deeper soil organic profiles (up to 300 cm) in EI mangroves compared to the other hydrogeomorphic settings in this study (Table 1). In estuarine mangroves, 62% of the total soil carbon stocks were distributed in deeper soil layers (>100 cm) rather than the upper layer (top 100 cm). By contrast, deeper soil layers across other mangrove settings only contributed 39% of the total soil carbon stock.

The overall mean of above- and below-ground live biomass carbon stocks (AGBC and BGBC) were 96 ± 65 and 17 ± 16 Mg C/ha, respectively, with relatively larger stocks observed in Bintuni Bay, Buruway and Etna compared to Kaimana ($p < .05$). Across hydrogeomorphic settings, AGBC was significantly different ($p < .05$), while BGBC was similar ($p = .41$; Table S3). We also observed the largest dead wood carbon stocks in Bintuni Bay (20 ± 14 Mg C/ha) and the lowest in Kaimana (2 ± 3 Mg C/ha; $p < .05$); however, significant variation between hydrogeomorphic settings was not observed ($p = .53$; Table S3).

Mangrove forest structural variables, such as basal area and tree density, varied significantly across undisturbed mangrove sites ($p < .05$; Figure 3a,c). Mean basal area in Bintuni Bay, Buruway and Etna Bay was greater than in Arguni and Kaimana ($p < .05$; Figure 3a). The highest mean (34 ± 13 m²/ha) tree density was observed in Bintuni Bay, while the lowest (13 ± 11 m²/ha) was in Kaimana ($p < .05$; Figure 3c). However, across hydrogeomorphic settings, basal area and tree density were not significantly different ($p > .05$; Figure 3b,d).

In addition, soil carbon density also differed significantly between sampling sites ($p < .05$; Figure 3e), but was similar across hydrogeomorphic settings ($p > .05$; Figure 3f). The largest mean soil carbon density was found in Bintuni Bay with 46 ± 10 g C/cm³. Soil bulk density mean varied significantly between sampling sites and hydrogeomorphic settings ($p < .05$; Figure 3g,h). Kaimana had the largest mean of soil bulk density (0.55 ± 0.14 g/cm³), while the lowest was observed in Arguni Bay (0.35 ± 0.15 g/cm³). Across hydrogeomorphic settings, EF mangrove had the greatest mean of soil bulk density (0.56 ± 0.24 g/cm³), and the lowest was found in the EI mangrove setting (0.42 ± 0.19 g/cm³). Similar to bulk density, soil carbon content was significantly different between sampling sites and hydrogeomorphic settings ($p < .05$; Figure 3i,j). The largest carbon content was observed in Arguni Bay ($19 \pm 11\%$) and EI mangrove setting ($15 \pm 10\%$). Furthermore, soil bulk and carbon densities increased significantly with soil depth ($p < .05$; Figure 4a,c). By contrast, soil carbon content was similar across

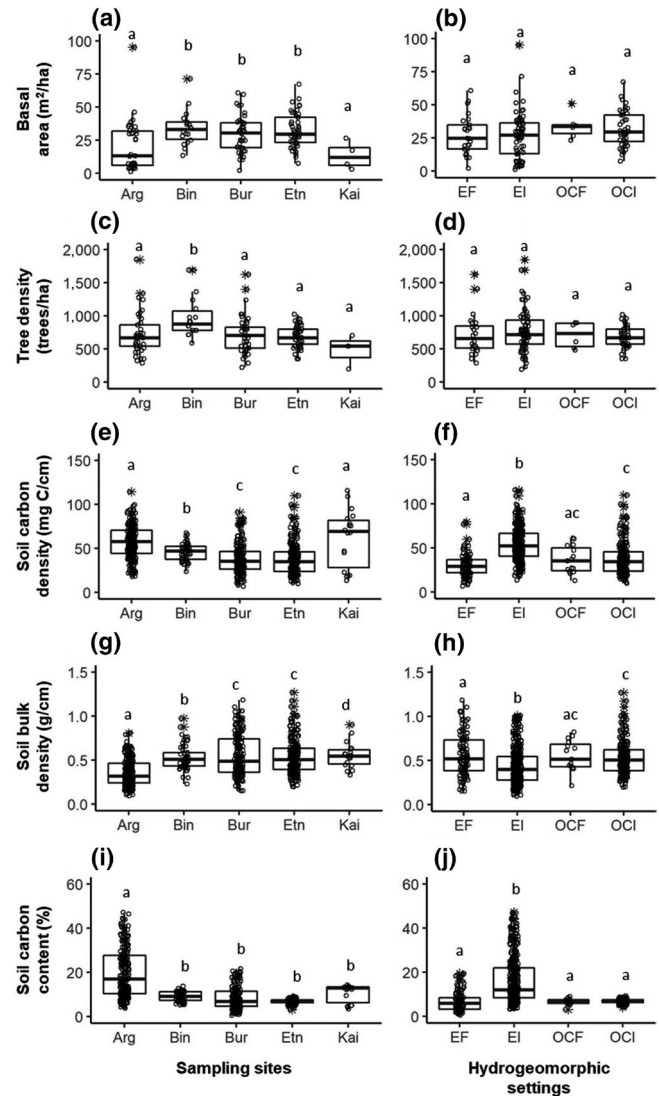


FIGURE 3 Variation of forest structures: (a, b) basal area and (c, d) tree density as well as variation of soil properties: (e, f) carbon density, (g, h) bulk density, and (i, j) carbon content across undisturbed mangrove sampling sites and hydrogeomorphic settings. Boxplot shows minimum, lower quartile, median, upper quartile and maximum values. Letters above boxplot bars denote significant difference among sites and hydrogeomorphic settings resulting from multiple comparison analysis. Arg, Arguni Bay; Bin, Bintuni Bay; Bur, Buruway; EF, estuarine fringe; EI, estuarine interior; Etn, Etna Bay; Kai, Kaimana; OCF, open coast fringe; OCI, open coast interior

depths ($p > .05$; Figure 4b). However, within the extended soil sample collection in Bintuni Bay (>100 cm depth), at approximately 150 and 300 cm, all soil properties (bulk density, carbon content and carbon density) were significantly different ($p < .05$; Table S3).

The best regression model identified in the generalized linear model analysis suggested that soil depth was the most important variable to predict variation in total ecosystem carbon stocks (indicated by the lowest p value), followed by stand basal area, soil carbon density and bulk density (Table S4). The 10 best multiple regression models (out of 446 possible models) indicate hydrogeomorphic

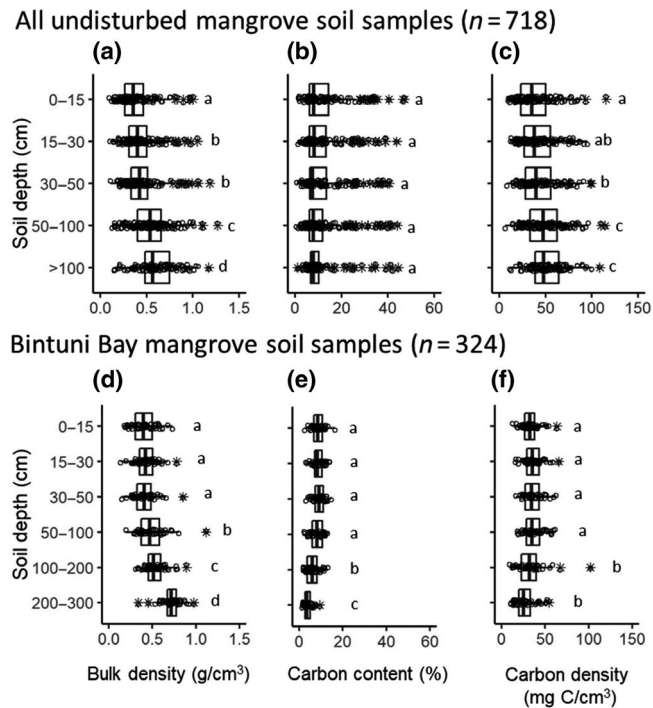


FIGURE 4 Variation of soil properties toward depths. Top panel presents (a) bulk density, (b) carbon content, (c) carbon density across standard depth interval, all for undisturbed sampling sites. Bottom panel shows (d) bulk density, (e) carbon content, (f) carbon density across extended sampling depths, up to 300 cm obtained from Bintuni Bay with assumed limited influence of above-ground harvesting and regeneration on soil properties (Figure 5b). Boxplot shows minimum, lower quartile, median, upper quartile and maximum values. Letters next to boxplot bars denote significant difference between depths resulting from multiple comparison analysis

setting, land-use change, soil depth, stand basal area and soil carbon density to be the optimal variables to describe variation in total ecosystem carbon stocks (Table S4). These variables were selected by all of 10 best models, whereas other variables such as soil bulk density was only selected by six models, soil carbon content by four models, and tree density as well as number of mangrove species by three models, respectively.

3.2 | Carbon stock loss and recovery following land-use changes

Rotational harvesting of mangrove forest in Bintuni Bay resulted in a nearly complete loss of live biomass carbon stocks and a 99% increase in dead wood (Figure 5a). The mean of dead wood carbon stocks at a 0-year-old post-harvest forest site was $40 \pm 15 \text{ Mg C}/\text{ha}$, compared to only $20 \pm 14 \text{ Mg C}/\text{ha}$ at undisturbed reference forests (Figure 5a). Overall, rotational forest harvesting generated 75% net carbon stock losses due to combined stock changes of live biomass and dead wood carbon pools (Figure 5b). By contrast, there was little significant change of soil carbon stocks resulting from rotational

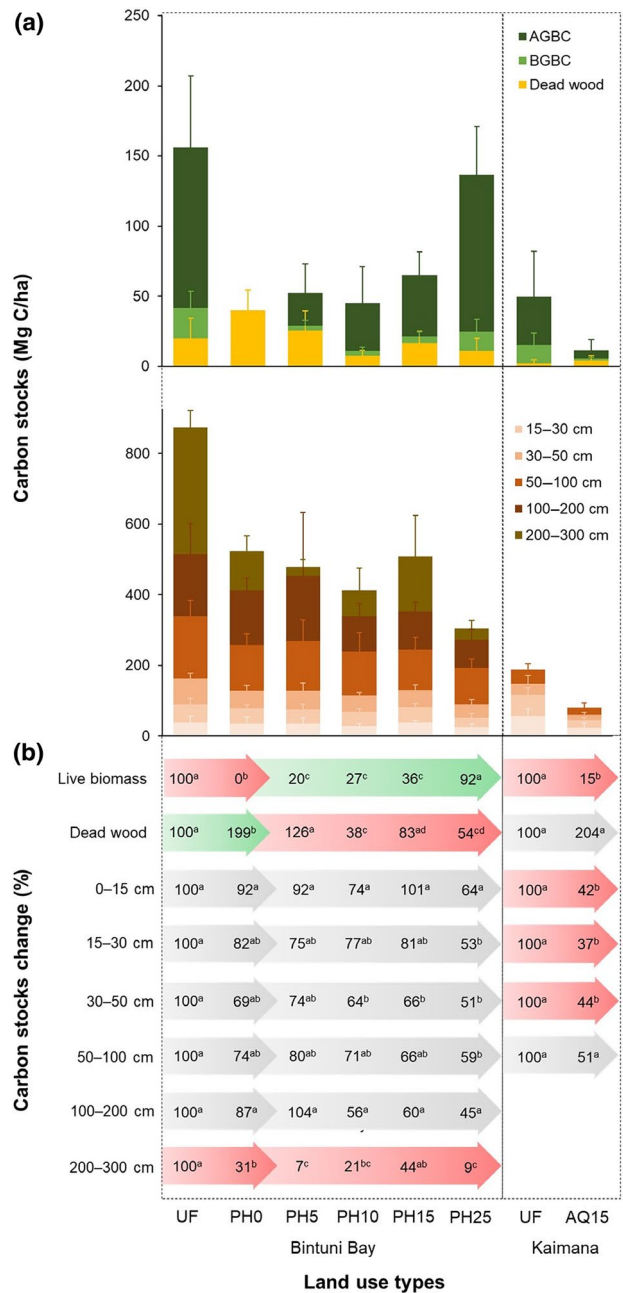


FIGURE 5 Carbon stocks across carbon pools and land-use types (panel a) and variation in carbon stock change in the percentage of the remaining carbon stock relative to undisturbed reference forests (panel b). Soil carbon stocks in panel (a) were standardized following soil mass equivalence at each depth layer. Green arrows indicate carbon stocks increase, red arrows show carbon stocks decrease and grey arrows denote no significant changes ($p > .05$). Letters next to the percentage change values in panel (b) indicate significant differences ($p < .05$) among carbon stock pool across land-use types at Bintuni and Kaimana. AQ15, aquaculture 15 years after conversion; PH0–PH25, mangroves 0–25 years post-harvest; UF, undisturbed mangrove forests

harvesting, particularly between 0 and 200 cm upper soil layers ($p > .05$; Figure 5a,b). Nevertheless, soil carbon stocks at the deepest soil layer (>200 cm) between these two land uses were significantly

different ($p < .05$; Figure 5b), in which we observed larger carbon stocks in undisturbed than in 0-year-old post-harvest forests.

Mangrove regeneration over 25 years resulted in a mean recovery of biomass carbon stocks of $3.6 \pm 1.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. Compared to reference sites, live biomass carbon stocks at 25-year-old regenerated forests were not significantly different ($p > .05$; Figure 5b). Across forests that had regenerated for 10 and 25 years, dead wood carbon stocks were lower than in reference forests ($p < .05$; Figure 5b). Carbon stocks at 0–200 cm upper soil layers across all regenerated forests were similar compared to reference stands ($p > .05$; Figure 5a,b).

In Kaimana, live biomass and soil carbon stocks were significantly different between sites converted to aquaculture and undisturbed reference sites ($p < .05$; Figure 5a,b). Mangrove conversion to aquaculture resulted in live biomass carbon stocks losses of 85% (Figure 5b). In addition, aquaculture conversion generated a soil carbon stocks decrease of ~60% at 0–50 cm soil layers (Figure 5b). Combining carbon stock losses from live biomass and soil carbon pools, mangrove to aquaculture conversion reduces carbon stocks by 66%.

4 | DISCUSSION

4.1 | Hydrogeomorphic settings control undisturbed mangrove carbon stocks

Across undisturbed mangroves in West Papua, Indonesia, variation in total ecosystem carbon stocks is strongly influenced by the underlying hydrogeomorphic setting. For example, in Bintuni and Arguni Bays, where mangroves are characterized by a tidally dominated estuarine setting, total carbon stocks were larger compared to those located in open coast settings, such as in Etna Bay (Figure 2). An estuarine mangrove setting is typically supported by extensive allochthonous sediment supply and resulting accommodation space, creating the spatial and vertical room within which mangrove sediments may accumulate (Woodroffe et al., 2016), leading to the maintenance of soil carbon burial rates over historical millennia timescales (Rogers et al., 2019). This pattern, however, may not be observed in open coast settings, typically characterized by a lower tidal range, steeper coastal profile and thus less accommodation space (Woodroffe et al., 2016). At the meso-scale, distinct hydrodynamic differences (tidal inundation and flushing) between fringe and interior forest locations also generated substantial carbon stocks variation, specifically within a large macro-tidal estuarine setting, such as in Bintuni Bay. Fringe mangrove locations are prone to seasonally driven sediment dynamics, whereas interior locations experience less tidal flushing, allowing persistent rates of organic-rich sedimentation and increased accumulated autochthonous carbon inputs (Krauss et al., 2014; Sasmito et al., 2020). As a result, El mangroves stored the largest ecosystem carbon stocks compared to the other hydrogeomorphic settings observed in this study (Figure 2b).

Similar to previous mangrove carbon stock assessments (Donato et al., 2011; Murdiyarso et al., 2015), the soil carbon pool accounted for the majority (89%) of carbon, relative to the other carbon pools, across mangrove settings (Figure 2). For instance, total carbon stocks in El mangrove sites consisted of 94% soil carbon, while across the rest of the mangrove settings, the soil carbon pool represented between 71% and 85%. The larger proportion of the soil carbon pool in El mangroves is attributed to the higher carbon content (Figure 3j) and deeper organic soil layers (Table 1), a function of the complex interaction between sediment supply, accommodation space, hydrodynamics and biomass productivity. Overall, our findings suggest that the hydrogeomorphic setting substantially controls soil carbon and therefore, total carbon stocks in mangrove ecosystems.

4.2 | Effect of soil properties and forest structure on carbon stocks

Comparison of the outcomes of multiple regression analyses suggests that total ecosystem carbon stocks are strongly influenced by variation in soil properties (soil depth, bulk density and carbon density), forest structure (basal area), hydrogeomorphic settings and land-use change. Soil depth was the most significant variable explaining variation in total ecosystem carbon stocks, suggesting that deeper soil depth layers have the larger carbon stocks. These findings are consistent with recent global scale assessments (Kauffman et al., 2020), in which carbon stock estimates could be double those currently reported if soil carbon stocks >100 cm are included in the blue carbon stock estimates. The results of our analyses also clarify that both hydrogeomorphic setting and land-use change are equally significant factors in contributing to variation in total ecosystem carbon stocks.

Soil physicochemical properties, including carbon density, soil bulk density and carbon content, are the important factors contributing to the variation in soil carbon stocks. Previous assessments of mangrove soil carbon stocks typically extrapolate the size of the soil pool to 300 cm (Adame et al., 2018; Donato et al., 2011; Kauffman, Heider, Cole, Dwire, & Donato, 2011), rather than use measured observations at these depths. Extrapolation of soil carbon to deeper soil depths is usually based on assessments of bulk density and carbon content from ~75 cm depth (midpoint between 50 and 100 cm). However, with collection of soil samples to 300 cm, as we achieved at Bintuni Bay, we found that carbon content in the deeper soil layers (>100 cm) was two to three times lower than in upper layers (>100 cm; Table S3). This pattern was also observed for bulk density, in which bulk density at ~300 cm was nearly double of that observed in 0–50 cm layers. Clearly, collection of samples from deeper soil layers enhances the precision of stock estimates and the understanding of soil carbon variability with depth. Despite high costs, high density replicated sampling at depth and across settings must be incorporated into carbon stock assessments. This will reduce uncertainties associated with variations in soil carbon over hydrogeomorphic settings and with future land-use changes.

In addition, AGBC between mangrove sites and settings was also significantly different (Table S3) despite tree density and basal area being similar among settings (Figure 3b,d). The variation of AGBC may be attributed to variation in species composition and the application of species-specific tree biomass allometric equations (Table S1). In contrast, BGBC was similar between mangrove settings (Table S3). In this case, species-specific equations were not fully applied because suitable species-specific equations from relevant geographical and climatic conditions were not available, specifically for multiple species including *Sonneratia* spp. and *Xylocarpus* spp. (Table S1). The variability in the dominant mangrove species among sites and settings results in variation in biomass carbon stocks. Our findings also suggest that future refinement of mangrove carbon stocks assessments requires improved tree allometric equations, particularly for the below-ground root carbon pool (Adame, Cherian, Reef, & Stewart-Koster, 2017).

4.3 | Mangrove harvesting and aquaculture conversion generate carbon stock losses

Our findings suggest that land management practices such as forest harvesting and small-scale aquaculture reduce carbon stocks substantially, with the degree of reduction dependent on the type of land-use change. This is similar to the broad conclusions derived from a recent global-scale systematic review and meta-analysis (Sasmito, Taillardat, et al., 2019) but extends this further by region-specific emissions factors. Within Bintuni Bay harvested forests, live vegetation biomass carbon stocks were nearly zero due to timber extraction. Nevertheless, not all vegetation was extracted successfully, leaving some dead stumps behind, and consequently there was a 100% increase in dead wood material left on the ground (Figure 5a). Our assessment was unable to quantify the dead biomass carbon located in the below-ground roots of logged stands, suggesting that further quantification of this carbon pool may improve current understanding of carbon stock loss associated with forest harvesting.

There was no statistical difference in soil carbon stocks of upper soil layers (0–200 cm) between logged forests and undisturbed reference sites, suggesting that most soil carbon stocks remain preserved due to minimal soil disturbance during the harvesting process. However, logged forest areas are continuously emitting GHGs as a result of decomposition of below-ground and dead biomass, as observed from mangrove clearing studies in the Caribbean (Lovelock, Ruess, & Feller, 2011) and Africa (Lang'at et al., 2014). These processes may be implied when we observed a decrease in dead wood carbon stocks after 5–10 years, following harvesting (Figure 5a). In summary, tree removal activities generate larger carbon stock losses within the biomass carbon pool rather than the soil carbon pool, despite uncertainty on the amount of direct GHG emissions.

Unlike forest harvesting, mangrove conversion into aquaculture generates carbon stocks loss from all carbon pools (Figure 5). While

carbon stock losses due to harvesting can be attributed mainly to loss from the biomass pool, aquaculture conversion reduces 85% of carbon stocks from the biomass carbon pool and ~60% of carbon stocks from soil (0–50 cm) carbon pools, similar to losses observed in the Dominican Republic (Kauffman et al., 2014). In addition, further soil carbon stock losses during aquaculture development are potentially unaccounted for. Specifically, fishpond development requires the removal of the top meter of sediments following mangrove forest clearing (Sidik & Lovelock, 2013). Therefore, mangrove conversion to other land uses, such as aquaculture, generates up to three times larger carbon stock losses compared to forest harvesting.

Our assessment reveals strong variation in mangrove carbon stocks between hydrogeomorphic settings, and therefore the degree of impact on carbon stocks and thus CO₂ emission may be dependent on the specific mangrove setting in which human disturbance occur. For instance, carbon stock loss caused by the same land-use change (e.g., aquaculture) may have greater impacts if aquaculture is developed over EI mangroves rather than mangroves in fringe or open coast setting. Quantifying carbon emissions from land-use change using the stock difference approach therefore requires careful selection of sampling sites, particularly pairing reference and treatment sites within a similar mangrove site and hydrogeomorphic setting.

4.4 | Carbon stock recovery following mangrove regeneration

While there is no obvious change in soil carbon stocks following harvesting, the differences in carbon stocks between some soil layers may be attributed to natural spatial variation. The carbon stocks recovery, however, was indicated by the increase in biomass carbon stocks following all regeneration years across the chronosequence (Figure 5a). The findings suggest that mangrove regeneration in the study area is more rapid compared to the global average of ~40 years (Sasmito, Taillardat, et al., 2019) and site-specific studies in Peninsular Malaysia (>40 years; Adame et al., 2018) and The Philippines (~50 years; Salmo, Lovelock, & Duke, 2013). The efficiency of carbon stock recovery could be driven by several factors: (a) climatic conditions, as Bintuni is located near the equator with high annual rainfall (>3,000 mm), which may drive higher productivity, reduce the occurrence of natural disturbances such as cyclones, and limit variation of annual temperature and humidity; (b) hydrogeomorphic setting, as the site is located in an estuarine geomorphic setting, characterized by nutrient-rich sediment and tall forest stands (Rovai et al., 2018; Simard et al., 2019); and (c) forest harvesting methodology, under which selective harvesting is applied in this study site (Sillanpää et al., 2017) rather than large-scale biomass removal.

4.5 | Implications for blue carbon policy and restoration

Indonesia's mangroves have previously been identified as a key contributor to its national carbon emissions, and a key solution

to emissions reduction (Murdiyarto et al., 2015). Accounting for ~10% of the world's mangrove area, Papuan mangroves can be an important aspect of nature-based climate change mitigation in Indonesia due to their high carbon stocks, and as such they have a role to play in Indonesia's nationally determined contributions (NDCs) to the Paris Agreement (Howard et al., 2017; Roe et al., 2019). In Indonesia's latest NDC, potential emissions and reductions from mangrove conversion and restoration are not separately included in accounts, but are amalgamated with other mineral soil forests under the forestry category (Government of Indonesia, 2017). Given the magnitude of soil carbon emissions from mangrove loss, and the role of mangroves in GHG management, policymakers have an opportunity to separate mangroves from other forests and account for their unique emissions profiles and removals ability, similar to current calculations made for biogenic peatlands. When carbon emissions associated with mangrove land-use change are not separately calculated, the magnitude of this ecosystems' impact on GHG emission management may be underestimated. While previous blue carbon knowledge gaps in Indonesia were associated with the availability of suitable emissions factor data (Murdiyarto et al., 2018), findings and data from this study, along with other studies from other islands such as Kalimantan (Arifanti et al., 2019) and Sulawesi (Cameron, Hutley, Friess, & Brown, 2019), could be used by policymakers to develop science-based policy and manage blue carbon emissions abatement at the national scale.

The influence of land-use change on carbon stocks shown in this study suggests that reducing disturbance to Papua's mangroves would be an important strategy to reduce Indonesia's carbon emissions from the land-use sector. Mangrove conservation would sustain the natural functions of mangroves as carbon sinks and minimize emissions from future land-use change. Papua's unprotected mangroves may face threats from proposed agricultural developments in the future (Richards & Friess, 2016). Therefore, policies should be developed to increase protected area coverage and prevent further mangrove conversion to other land uses. Such actions could contribute efficiently to Indonesia's GHG emissions reduction targets because the carbon loss per area and associated emissions of mangrove deforestation are between two and five times larger—depending on hydrogeomorphic setting—than emissions generated by terrestrial tropical deforestation.

This study shows that mangrove restoration, if conducted at an adequate scale, has the potential to contribute to Indonesia's NDCs by increasing mangrove carbon stocks and offsetting anthropogenic GHG emissions. This has also been shown at the site scale for other parts of Indonesia (Cameron et al., 2019). There is growing interest in utilizing carbon removals by mangroves in Indonesia and elsewhere to finance restoration activities, by trading carbon credits through the Kyoto Protocol's Clean Development Mechanism or voluntary Payments for Ecosystem Services schemes (Locatelli et al., 2014). However, there are clear constraints associated with the success rates of mangrove restoration (Kodikara, Mukherjee, Jayatissa, Dahdouh-Guebas, & Koedam, 2017) and their costs

(Bayraktarov et al., 2016). Current mangrove restoration programs place a lot of attention on the low success rates of planted seedlings because planting is conducting in inappropriate habitats adjacent to mangroves (e.g., mudflats, beaches) without regard for their hydrogeomorphic suitability (Lee, Hamilton, Barbier, Primavera, & Lewis, 2019). This study shows that the effectiveness of carbon stock recovery following mangrove regeneration is dependent on biophysical factors such as the coastal hydrogeomorphic setting. However, mangrove restoration projects are often forced into unsuitable locations due to factors such as land-use management, land tenure and inappropriate planting incentives, and these remain major constraints to successful mangrove restoration (Lovelock & Brown, 2019; Wodehouse & Rayment, 2019). Therefore, both land management and biophysical data should be equally incorporated for effective mangrove restoration to recover natural mangrove functions efficiently.

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AUTHORS' CONTRIBUTIONS

S.D.S. led the study design, drafting of all figures and tables and writing of the paper with substantial contributions from D.A.F., L.H., D.M., T.W., C.E.L., M.A.H., J.H. and M.S. S.D.S., M.S., M.A.H., S.B., M.F.S., F.S., B.B.H., W.Y.M., V.I.S., H.H., S.T., S., J.D.N., T.P., N.W., B., V.N., R.N.Y., C.D.H. and J.H. performed fieldwork. M.S. and M.H. contributed unpublished datasets, and T.W. and P.Z.E. contributed the map of mangrove hydrogeomorphic settings. S.D.S., M.A.H., J.S.R. and H.H. analyzed and interpreted data. S.D.S. performed statistical analyses.

DATA AVAILABILITY STATEMENT

All raw data from this study are accessible through the CIFOR Dataverse digital repository (Sasmito et al., 2019a, 2019b, 2019c).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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