Carbon stocks of intact mangroves and carbon emissions arising from their conversion in the Dominican Republic

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Abstract. Mangroves are recognized to possess a variety of ecosystem services including high rates of carbon sequestration and storage. Deforestation and conversion of these ecosystems continue to be high and have been predicted to result in significant carbon emissions to the atmosphere. Yet few studies have quantified the carbon stocks or losses associated with conversion of these ecosystems. In this study we quantified the ecosystem carbon stocks of three common mangrove types of the Caribbean as well as those of abandoned shrimp ponds in areas formerly occupied by mangrove-a common land-use conversion of mangroves throughout the world. In the mangroves of the Montecristi Province in Northwest Dominican Republic we found C stocks ranged from 706 to 1131 Mg/ha. The medium-statured mangroves (3-10 m in height) had the highest C stocks while the tall (>10 m) mangroves had the lowest ecosystem carbon storage. Carbon stocks of the low mangrove (shrub) type (<3 m) were relatively high due to the presence of carbon-rich soils as deep as 2 m. Carbon stocks of abandoned shrimp ponds were 95 Mg/ha or $\sim 11\%$ that of the mangroves. Using a stock-change approach, the potential emissions from the conversion of mangroves to shrimp ponds ranged from 2244 to 3799 Mg CO₂e/ha (CO₂ equivalents). This is among the largest measured C emissions from land use in the tropics. The 6260 ha of mangroves and converted mangroves in the Montecristi Province are estimated to contain 3 841 490 Mg of C. Mangroves represented 76% of this area but currently store 97% of the carbon in this coastal wetland (3696722 Mg C). Converted lands store only 4% of the total ecosystem C (144778 Mg C) while they comprised 24% of the area. By these metrics the replacement of mangroves with shrimp and salt ponds has resulted in estimated emissions from this region totaling 3.8 million Mg CO₂e or $\sim 21\%$ of the total C prior to conversion. Given the high C stocks of mangroves, the high emissions from their conversion, and the other important functions and services they provide, their inclusion in climate-change mitigation strategies is warranted.

Key words: blue carbon; carbon stocks; climate-change mitigation; coastal ecosystems; CO₂e emissions; land use; mangroves; REDD+; shrimp ponds.

INTRODUCTION

Mangrove forests occur along the coasts of most major oceans in at least 124 countries. Renowned for an array of ecosystem services including fisheries and fiber production, sediment regulation, and storm/tsunami protection, mangroves are nevertheless declining due to aquaculture expansion, agricultural development, overharvest, and development (Alongi 2002, Polidoro et al. 2010, Giri et al. 2011). A 30–50% decline in land area over the past half century has prompted estimates that mangroves may functionally disappear in as little as 100 years (Valiela et al. 2001, Duke et al. 2007). About 185 000 ha were lost every year in the 1980s (a net loss of 1.0% per year; FAO 2007). Recently, the rate of loss appears to have slowed down, although it is still high.

The net mangrove deforestation rate in the 1990s was 0.72% and was 0.66% during the 2000–2005 period (FAO 2007). This decline may reflect an increased awareness of the value of mangrove ecosystems (FAO 2007) or the complete conversion of the most accessible sites. In addition to losses of ecosystem services, the global emissions from mangrove degradation have been estimated to be as much as 0.12 Pg C/yr (Donato et al. 2011). This is equivalent to almost 10% of the global emissions associated with tropical forests, although mangroves occupy <1% of the land area of tropical forests.

In the insular Caribbean, mangroves were estimated to cover about 762 250 ha in 1990 (Ellison and Farnsworth 1996). Mangroves have been estimated to occupy about 21 215 ha in the Dominican Republic. They are widespread, particularly along the northern coasts (Spalding et al. 2010), with large contiguous areas in the northwestern corner within the Province of Montecristi, the location of our present study.

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While the values and ecosystem services of mangroves are well known, few data exist for carbon stocks in Latin America and even fewer on the declines in C stocks or emissions that would arise from land-use conversion of mangroves. This is especially true in the Caribbean where studies of aboveground biomass have been conducted, but few studies have quantified the total ecosystem carbon stocks of the mangroves. This is important as many studies have reported that belowground C pools account for 49-98% of the total ecosystem C stock in mangroves (Donato et al. 2011, Adame et al. 2013). In addition, few measurements have been made of the C stocks of land uses that replace mangroves, and the associated emissions that arise from land-cover change. Given that mangroves have been characterized as having a high C density coupled with a high rate of deforestation, there is an increased interest in including mangroves as part of climate-change mitigation strategies that would reduce the anthropogenic emissions of greenhouse gasses. To effectively apply these strategies, it is important to quantify and understand the emission factors associated with changes in land use, so that baselines can be set for countries to participate in future climate-change mitigation strategies such as reduced emissions from deforestation and degradation (REDD+; Murdiyarso et al. 2012).

The objectives of this study were to quantify the ecosystem carbon stocks of the largest mangrove ecosystem complex in the Dominican Republic and identify baseline C stocks in a manner that would function as part of a country-level REDD+ program. To accomplish these objectives, we (1) identified the current and converted mangrove extent of the region, (2) stratified mangroves based upon geomorphology, structure, and land use, (3) measured the total ecosystem C stocks within each type, and (4) scaled the ecosystem C stocks to the landscape scale to estimate total stocks and losses due to conversion. Our hypotheses were that C stocks would differ among mangrove types and land uses, and forest structure would be indicative of ecosystem pools (i.e., the largest C stocks would be found in the tall forested mangroves). Further, we predicted that C losses from land-cover change would be high relative to land use in upland ecosystems because of large losses of both aboveground and belowground pools.

METHODS

Study site

The study area is located in the northwestern Dominican Republic, following the coastline of the province of Montecristi from ~ 3 km east of the Haiti border to ~ 15 km northeast of the town of Montecristi (Fig. 1). The area is within and surrounding the Montecristi National Park. The coastal wetlands of the area are flooded by a mixture of seawater from tidal fluxes and water from rivers that flow into the wetlands. Mangroves in Montecristi were separated into structural classes similar to those defined for other Caribbean mangroves by Adame et al. (2013) and Murray et al. (2003): (a) tall mangroves with a mean height >10 m and usually occurring on the margins of rivers and estuaries; (b) medium mangroves that form dense stands of trees of 3 to 10 m in height, usually as interior forest, and (c) low mangroves, composed of dense stands of trees whose height is <3 m and occurring inland of coastal margins (Table 1). In addition to intact mangroves, we sampled abandoned shrimp ponds. The shrimp ponds were mangrove forests until they were cleared in 1983. The shrimp ponds were actively used for 10 years until 1993. The ponds were then abandoned and not used from 1993 to the time of sampling in 2012. Levees continued to block freshwater and tidal inputs into these sites at the time of sampling.

Rainfall in the region averages 672 mm/yr with the majority falling during the months of June to October. The mean annual temperature is 26.3°C (Oficina Nacional de Meteorologia, Dominican Republic). The soils in the mangrove were field classified as a fine silt mixed isohyperthermic Typic Hydraquent.

Field sampling

We determined the composition, structure, and ecosystem carbon stocks of 12 different coastal wetlands including three sites each of: (1) tall mangroves; (2) medium mangroves; (3) low mangroves; and (4) abandoned shrimp ponds. Within each site, ecosystem C stocks (above- and belowground) were measured following methods outlined by Kauffman and Donato (2012). At each tall and medium mangrove site, six 7-m fixed-radius plots were established 25 m apart along a 125-m transect established in a perpendicular direction from the marine ecotone. In the low mangroves, 2 m fixed-radius plots were established in a similar manner but at 10-m intervals. Only five plots were sampled in the shrimp ponds that were covered by bare ground or a sparse cover of halophytic vegetation. At each plot we collected data necessary to calculate total C stocks derived from standing tree biomass, downed wood (dead wood on forest floor) and soils to the depths of the marine sands.

Biomass of trees and shrubs

Four species of mangroves occur throughout the Caribbean: *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia germinans* (L.) Stearn (Avicenniaceae), *Laguncularia racemosa* (L.) Gaertn., and *Conocarpus erectus* L. (Combretaceae). We encountered the first three in the plots that we sampled; *C erectus* was observed on the upland edges of the mangroves. Composition, tree density, and basal area in tall and medium mangroves were quantified through measurements of the species and diameter at 1.3 m height (dbh) of all trees rooted within each plot of each transect. Plot size for tree measurements in the tall and medium mangroves was 154 m² (7 m radius) for trees >5 cm dbh

and a nested plot with a radius of 2 m for trees with a dbh of <5 cm. The diameter of *R. mangle* trees was measured above the highest prop root. For the mangrove plants that were <2 m in height in the low mangroves, the diameter of the main branch was measured at 30 cm from the ground (D_{30}). Additionally, in the low mangroves height for each individual was measured.

Allometric equations were used to calculate tree biomass for each site (Appendix A). In the tall and medium mangroves we used species specific formulas from French Guinea provided in Fromard et al. (1998). Aboveground biomass of individuals in the low mangroves, was determined using equations developed in Puerto Rico by Cintron and Shaeffer-Novelli (1984) that used mainstem diameter and tree height. Belowground root biomass for mangrove trees was calculated using the formula by Komiyama et al. (2005). Tree C was calculated from biomass by multiplying by a factor of 0.48 for aboveground and 0.39 for belowground biomass (Kauffman and Donato 2012).

Standing dead trees were included in aboveground biomass calculations. For each dead tree, the stem diameter was measured and assigned to one of three decay classes: Status 1, dead trees without leaves; Status 2, dead trees without secondary branches; and Status 3, dead trees without primary or secondary branches (Kauffman and Donato 2012). The biomass for each tree status was calculated using allometric equations of plant components. For dead trees of Status 1, biomass was calculated as the total dry biomass minus the biomass of leaves. The biomass of trees of Status 2 was calculated for R. mangle as the sum of stem, branches and prop roots, and for L. racemosa and A. germinans as the sum of stem and branches. Finally, the biomass of trees of Status 3 was calculated as the biomass of the mainstem only. This also required estimation of the dead tree height in this decay class. Standing dead trees in the low forests were very rare and, if present, were included with live trees.

Downed wood

We used the planar intersect technique adapted for mangroves to calculate mass of dead and downed wood (Van Wagner 1968, Kauffman and Donato 2012). At the center of each plot, four 14-m transects were established. The first was established in a direction that was offset 45° from the azimuth of the main transect. The other three were established 90° clockwise from the first transect. At each transect, the diameter of any downed, dead woody material (fallen/detached twigs, branches, prop roots, or stems of trees and shrubs) intersecting the transect was measured. Wood debris \geq 2.5 cm but < 7.5 cm in diameter (hereafter "small" debris) at the point of intersection was measured along the last 5 m of the transect. Wood debris \geq 7.5 cm in diameter (hereafter "large" debris) at the point of intersection was measured from the second meter to

the end of the transect (12 m in total). Large downed wood was separated in two decay categories: sound and rotten. Wood debris was considered rotten if it visually appeared decomposed and broke apart when kicked.

We used data of specific gravity of downed wood determined for Caribbean mangroves of the Yucatan, Mexico, and reported by Adame et al. (2013). Using the specific gravity for each group of wood debris, biomass was calculated using formulas reported in Kauffman et al. (2011) Downed wood was converted to C using a factor of 0.50 (Kauffman and Donato 2012).

Soil carbon and nutrients

At each plot, soil samples were collected for bulk density and nutrient concentration using a peat auger consisting of a semi-cylindrical chamber of 6.4 cm radius. This auger is efficient for collecting relatively undisturbed cores from wet soils under mangroves (Donato et al. 2011). The core was systematically divided into depth intervals of 0-15 cm, 15-30 cm, 30-50 cm, 50–100 cm and >100 cm (if parent materials were not encountered before 100 cm depth). Samples of a known volume were collected in the field, dried to constant mass, and then weighed to determine bulk density. The depth to the parent materials (marine sediments/sands) was measured at three locations near the center of each plot using a graduated aluminum probe. The inference limit of the study was 2.5 m for depths exceeding the probe length.

In the laboratory (Oregon State University Central Analytical Laboratory), the concentrations of C and N were determined using the dry combustion method (induction furnace) with a LECO CNS-2000 Macro Analyzer (LECO Corporation, St. Joseph, Michigan, USA). Bulk density and carbon concentration were then combined with plot-specific soil depth measurements to determine the soil C stocks.

Differences among biomass and carbon stocks among vegetation types (tall, medium, and dwarf mangroves, and shrimp ponds) were tested with analysis of variance (ANOVA). If the ANOVA was significant, a Tukey HSD test was performed to determine which means were significantly different.

The study-area boundaries were delineated using aerial photo interpretation, extensive ground truthing and image analysis of Landsat imagery (USGS 2011). The wetlands of Montecristi included mangroves, mudflats, open water, and areas that were converted from mangroves to other land uses (e.g., salt and shrimp ponds). A rapid, supervised maximum-likelihood classification was conducted in the GIS to develop a range of image-band responses for tall, medium, and low mangroves, mud flats, converted areas, and open water (ESRI 2012). We calculated the total C stock of the region using the areal extent of each cover type multiplied by the mean C stock derived from the field data. Changes in ecosystem C stocks (emissions estimates) from land conversion were calculated as the



FIG. 1. Vegetation cover of the Montecristi wetland study area, northwestern Dominican Republic. The black star in the inset map is the approximate location of the study area (19.7666 N, 71.6919 W, UTM). Exact coordinates or all sampled plots can be found in Appendix B.

TABLE 1. Generalized descriptions of tall, medium, and low mangroves (mangle alta, media, and enano, respectively, in Spanish) of the mangroves of Montecristi, Dominican Republic.

	Feature						
Mangrove type	Canopy height (m)	Canopy tree diameter (cm)	Canopy tree density (no./ha)	Downed wood	Geomorphic position	Salinity (ppt)	Composition
Tall	>10	>5	dense (747–1039)	abundant	fringing, riverine edge	25–26	Rhizophora, Laguncularia, Avicennia
Medium	3–10	most <5	extremely dense (32000-72000)	scarce	basin, interior zones	33–36	Rhizophora, Laguncularia
Low	<3	most <2	extremely dense (13 000-92 000)	practically absent	basin, tidal flats, interior zones	42–51	Rhizophora, Avicennia



FIG. 2. Plant carbon stocks of tall, medium, and low mangroves of Montecristi, Dominican Republic, by sampling site. Error bars show +SE of the total aboveground stock.

carbon stocks in intact mangroves minus the carbon stocks of abandoned shrimp ponds.

RESULTS

Aboveground biomass and structure

Tall mangroves tended to occupy the land-water ecotone, while medium and low mangroves were most common in the interior and upland edges away from open water. *Rizophora mangle* was the most abundant mangrove species at all sampled sites with *Lagunularia racemosa* and *Avicennia germinans* present in lower abundances. While composition did not vary greatly, structure among the three mangrove types was dramatically different (Fig. 2, Tables 1 and 2). The tall mangroves exceeded 10 m while few individuals in low mangroves exceeded 3 m in height. Viable propagules were observed on individuals in all communities.

Density varied greatly among the mangrove community types with a mean tree density of ~ 900 trees/ha in the tall mangrove and >42000 trees/ha in medium and low mangrove (P = 0.03; Table 2). R. mangle comprised >99% of the individuals in the sampled low mangroves. In the medium mangroves, R. mangle averaged 88% of the live trees while L. racemosa comprised 12% of the density, though because of its larger stature contributed 40% of the tree mass of a site. Similarly in the tall mangrove, R. mangle consisted of 90% of the trees measured and L. racemosa accounted for about 8% of the trees measured. While the plots we sampled were dominated by R. mangle, there were communities apparent from both remote-sensing imagery and from observation in the field that were dominated by A. germinans (both tall and low mangrove). Both L. racemosa and A. germinans tended to be more abundant in areas away from the marine ecotone.

Among all of the sampled stands, there was almost a 40-fold difference in the total plant mass consisting of live and dead materials and above- and belowground biomass. Total plant mass ranged from a mean of 14 Mg/ha in the low mangrove at the Final site to 414 Mg/ ha in the tall mangrove at the Alta Tres site (Table 2). Live trees comprised the vast majority of this mass especially in low and medium mangroves. Downed wood and dead trees were a significant component only

TABLE 2. Density and mass of mangroves of the Montecristi National Park, Dominican Republic.

		Mangrove biomass, by component (Mg/ha)				
Plot sample site	Density (no./ha)	Live tree	Dead tree	Dead wood [†]	Total aboveground	
Low mangrove						
El Morro Granja Final Mean	$21 619 \pm 6 554 \\ 13 396 \pm 1 322 \\ 92 178 \pm 15 196 \\ 42 397 \pm 25 003$	9.0 ± 2.8 5.5 ± 1.1 21.1 ± 10.3 11.9 ± 4.7	$\begin{array}{c} 0\\ 0\\ 0\\ 0 \pm 0 \end{array}$		9.03 5.48 21.12 11.9 ± 4.7	
Medium mangrove			• – •			
Mediano Sur Laguna Media Guinea Media Mean	$\begin{array}{r} 71692\pm14157\\ 54102\pm13948\\ 32264\pm8271\\ 52686\pm11404 \end{array}$	$\begin{array}{c} 62.8 \pm 11.5 \\ 58.5 \pm 12.8 \\ 41.4 \pm 7.3 \\ 54.2 \pm 6.5 \end{array}$	$\begin{array}{c} 0.1 \pm 0.1 \\ 2.6 \pm 1.3 \\ 7.2 \pm 6.6 \\ 3.3 \pm 2.1 \end{array}$	$\begin{array}{c} 3.24 \ \pm \ 1.63 \\ 2.89 \ \pm \ 1.05 \\ 2.82 \ \pm \ 1.33 \\ 3.0 \ \pm \ 0.1 \end{array}$	66.14 63.99 51.42 60.5 ± 4.6	
Tall mangrove						
Tapion Balsa Alta Alta Tres Mean	$\begin{array}{r} 1039\pm120\\ 747\pm219\\ 909\pm442\\ 898\pm85 \end{array}$	$\begin{array}{r} 173.2 \pm 12.8 \\ 277.2 \pm 55.9 \\ 271.7 \pm 39.2 \\ 240.7 \pm 33.8 \end{array}$	$\begin{array}{c} 18.6 \pm 9.2 \\ 4.2 \pm 1.8 \\ 20.8 \pm 11.7 \\ 14.5 \pm 5.2 \end{array}$	$\begin{array}{c} 19.92 \pm 3.90 \\ 26.37 \pm 4.82 \\ 12.89 \pm 2.80 \\ 19.7 \pm 3.9 \end{array}$	$\begin{array}{r} 211.72 \\ 307.77 \\ 305.39 \\ 275.0 \pm 31.6 \end{array}$	

Note: The data are plot means \pm SE.

† Large wood debris was largely absent from the low mangrove and therefore not measured.

in the tall mangrove comprising about 12.5% of the total aboveground biomass.

In the low mangrove stands the ratio of the aboveground to belowground biomass was 0.81. In contrast, the aboveground : belowground ratio of the tall mangrove was 3.04 where mean total aboveground biomass was 275 Mg/ha and belowground was 91 Mg/ ha (Table 2).

Mean plant carbon stocks were 161, 47, and 10 Mg/ha for tall, medium and low mangroves, respectively, and were significantly different among the plant communities ($P \le 0.01$). The plant carbon of abandoned shrimp ponds was negligible and not measured. In these sites, vegetation ranged from a sparse cover of regenerating *A. germinans*, to an open cover of salt-tolerant herbs, to bare ground (salt flats).

Soils

Mean depths of the organic-rich soils to the marine sands ranged from 175 to 230 cm for the mangroves (Appendix B). In contrast the soil depth of abandoned shrimp ponds was significantly lower, with a mean of 71 cm. Variation was quite high among stands within the tall and low mangroves. In the tall mangroves the soil depth ranged from 120 to 211 cm. Similarly, in the low mangroves soil depth ranged from 66 to at least 250 cm (the inference limit of the soil probe), which was the widest range in depths among the mangroves, with the deepest mean soil depths, and in the highly disturbed abandoned shrimp ponds with the shallowest soils (Appendix B).

We found relatively high soil-carbon concentrations in mangroves above the marine sands. Carbon concentration of the surface soils (0-15 cm) of the mangroves was quite high at all mangroves, exceeding

TABLE 2. Extended.

Mangrove biomass, by component (Mg/ha)						
Belowground, live	Belowground, dead	Total plant				
$\begin{array}{c} 14.85 \pm 4.40 \\ 9.05 \pm 1.51 \\ 19.98 \pm 3.85 \\ 14.6 \pm 3.2 \end{array}$	$\begin{matrix} 0\\0\\0\\0 \pm 0\end{matrix}$	$23.88 \\ 14.53 \\ 41.10 \\ 26.5 \pm 7.8$				
$58.81 \pm 3.35 \\ 44.34 \pm 6.19 \\ 31.22 \pm 3.34 \\ 44.8 \pm 8.0$	$\begin{array}{l} 0.29 \pm 0.03 \\ 1.66 \pm 0.94 \\ 3.65 \pm 3.31 \\ 1.9 \pm 1.0 \end{array}$	$125.24 \\ 109.99 \\ 86.29 \\ 107.2 \pm 11.3$				
$\begin{array}{c} 72.34 \pm 8.09 \\ 100.28 \pm 18.93 \\ 99.11 \pm 10.31 \\ 90.6 \pm 9.1 \end{array}$	$\begin{array}{c} 10.37 \pm 4.28 \\ 4.04 \pm 2.02 \\ 9.11 \pm 3.30 \\ 7.8 \pm 1.9 \end{array}$	$294.43412.09413.61373.4 \pm 39.5$				

26% in the medium mangroves and >13% for low and tall mangroves (Appendix B). Relatively high carbon concentrations existed throughout the soil profile. For example, in the Guinea Media and Medianao Sur medium-mangrove sample sites the soils in the top meter exceeded 20% C concentration. The deeper horizons were substantially lower yet still relatively high at $\sim 9\%$ C (Appendix B). Nitrogen concentration tended to be highest in those samples with the highest concentration of C. Bulk density was inversely proportional to C concentration; samples with the lowest C concentration had generally higher bulk densities and tended to be associated with the deepest samples. There were some apparent differences in the C concentration among the mangrove types. For example, the surface soil concentration of the low mangrove was always <17% while those of the medium mangroves exceeded 25%. Throughout the soil profile, soil C concentration of the low mangrove was lower at the same depths than the medium mangroves.

The abandoned shrimp ponds were surrounded by mangroves and were of a similar geomorphology. However, soils in abandoned shrimp ponds were quite different than those of the mangroves (Appendix B). Carbon concentrations of the surface soils of the shrimp ponds averaged an order of magnitude lower than those of mangroves ($\leq 2.0\%$; Appendix B). While the bulk density of mangrove soil surfaces rarely exceeded 0.30 g/ cm³, those of the shrimp ponds were > 1.27 g/cm³. Even the deepest of soil samples of most of the mangroves were higher in C and N and lower in bulk density than the surface samples of the shrimp ponds. While the soils of the shrimp ponds were moist and some had standing water, tidal and freshwater inputs were limited by the presence of abandoned levees surrounding the ponds.

The relatively high concentration of C throughout the profile of the mangroves resulted in high carbon stocks. Carbon mass of the soils of the mangroves ranged from 262 Mg/ha in the Morro Bajo low-mangrove sample site to 1136 Mg/ha in the Laguna Media medium mangrove site. The mean soil C pools for the tall, medium, and low mangroves were 546, 1084, and 713 Mg C/ha, respectively. The relatively deeper soils coupled with higher C concentration resulted in the higher C pools in medium compared to tall mangroves (P < 0.001). These differences are likely due to the geomorphic conditions of the sites, with tall mangroves being on the water edge and likely younger and subject to greater disturbances by storm surges and flooding. There was a high degree of variation within the low mangroves with a range in soil C pools from 262 to 919 Mg C/ha. Even at greater depths for all of the sampled mangroves, the C density (carbon mass per unit of soil) remained high due to the increased bulk density.

Ecosystem carbon stocks

The mean total ecosystem carbon stock of the Montecristi mangroves was 853 Mg/ha (Fig. 3). In



FIG. 3. Total ecosystem carbon stocks (mean + SE) of mangroves and abandoned shrimp ponds of Montecristi, Dominican Republic. Error bars are +SE of the total ecosystem stock (aboveground and belowground). Differences between the ecosystem C stocks of shrimp ponds and all mangroves are highly significant (P = 0.001).

contrast, the mean total ecosystem C stock of the abandoned shrimp ponds was significantly lower at 95 Mg/ha (P = 0.001; Fig. 3). The C stocks of shrimp ponds were only about ~11% of that of the mangroves. This represents a potential loss of 661–1135 Mg C/ha when mangroves are converted to shrimp ponds.

Forest stature was not necessarily a good indicator of ecosystem C stocks. Unlike our predictions, tall mangroves were lower in ecosystem C stocks (707 Mg/ha) than the lower statured medium mangroves (1131 Mg/ha; P < 0.01). Low mangroves were similar to ecosystem C stocks of the tall mangroves (733 Mg/ha). In all sites soil carbon comprised the overwhelming majority of the ecosystem C stock, accounting for 77% of the total in tall mangrove and >96–99% in medium and low mangroves (Fig. 3).

Landscape-scale carbon stocks

The 9171-ha Montecristi wetland complex is a mosaic of mangroves, areas converted for land use, open water, and mud flats (Fig. 1). Approximately 6260 ha is vegetated land, with a mangrove cover of 4743 ha (76%) and 1516 ha (24%) in converted lands. We estimated the total C stock of the Montecristi wetland is 3841 490 Mg C (excluding both the unsampled C in mudflats and open water). Mangroves currently store an estimated 97% of the carbon of this area (3 696 722 Mg C). Medium mangroves accounted for only 12% of the land area (748 ha), but stored 22% of the total ecosystem C. Tall mangroves covered 37% of the area (2317 ha) and stored 43% of the total ecosystem C for the Montecristi wetland. Low mangroves covered 27% of the area (1678 ha) and comprised 32% of the ecosystem C stock.

Converted lands were estimated to be 24% of the vegetated area (1516 ha) but stored only 4% of the total ecosystem C (144768 Mg C). This contrasts with medium mangroves, which covered about half as much land but stored more than five times the mass of carbon.

Determining the loss of C from land-cover change is difficult due to an inexact knowledge of the historic cover and C stocks of areas under land use. Using the difference of 683.9 Mg/ha from the weighted average of all sampled mangroves and the mean of sampled abandoned shrimp ponds, we calculated a conservative estimate of 1 036 971 Mg C lost due to conversion of mangrove to cultivated salt ponds, shrimp ponds, and other uses. This loss translates to a potential decline from ~4.9 million Mg C to the current 3.8 million Mg C, or a loss of 21% of the potential ecosystem carbon stocks of the Montecristi wetlands since conversion.

DISCUSSION

Aboveground biomass

There was a tremendous range and variability in the aboveground forest structure and biomass of the mangroves sampled in this study. Mangrove density ranged from 747 trees/ha in the Balsa Alta tall-mangrove site to >92000 trees/ha in the Final low-mangrove site. The tree density of tall mangroves of this study (mean of 898 trees/ha) was similar to tree densities reported for tall mangroves of the Samana Bay, on the northcentral coast of the Dominican Republic (Sherman et al. 2003); they reported the aboveground biomass of 50-year old tall mangroves ranged from 124 to 384 Mg/ha with a mean of 234 Mg/ha. This is similar to the range of tall mangroves in our present study (212-305 Mg/ha; Table 2). In the Samana Bay mangroves, Sherman et al. (2003) also found that aboveground biomass of the forests was higher in the inland edge than on coastal fringe suggesting that our estimates of C stocks for tall mangrove that were sampled only at the fringe would be conservative or low for the stocks of tall mangroves further inland.

Forest structural differences among stands were also apparent by the tremendous range in aboveground biomass of the mangroves of Montecristi. The total aboveground biomass of different mangrove stands ranged from 5.5 to 305 Mg/ha in our present study. In mangroves of Bocas del Toro, Panama, Lovelock et al. (2005) reported that mangrove biomass varied over 20fold (8–194 Mg/ha). These mangroves were also dominated by *Rhizophora mangle* and were similar in density and height ranges to those measured in our present study.

Few studies on ecosystem C stocks have been conducted in the Caribbean. Adame et al. (2013) reported ecosystem carbon stocks for Caribbean mangroves of Mexico to be 287 Mg/ha for low mangrove, 546 Mg/ha for medium mangrove, and 914 Mg/ha for April 2014

tall mangrove. Unlike the mangroves of this study, the tall mangroves in Mexico had the largest C stocks. The low mangroves on karstic substrates in Mexico were similar in structure and composition to the mangroves of our present study but ecosystem carbon stocks were much lower due to shallower organic soils. Carbon concentrations of the surface soil horizons were also generally lower in the Mexican Caribbean mangroves. Soil C in the low mangroves of Mexico ranged from 205 to 362 Mg/ha. This is similar to the soil C pool of the Granja Bajo site (262 Mg/ha; Appendix B) but much lower than the other low mangroves (≥845 Mg/ha).

We found that the C stocks of the abandoned shrimp ponds were dramatically lower than that of the mangroves (P = 0.001). Assuming that these sites were formerly mangrove, conversion resulted in large losses of C stocks. Vegetation cover of the abandoned sites ranged from being devoid of cover to a sparse cover of halophytic species or Avicennia germinans. The abandoned levees surrounding the shrimp ponds still eliminated tidal flow into the sites and prevented runoff offsite. Soil C in abandoned shrimp ponds was lower throughout the soil profile. Losses of the carbon could be from the actual construction of the ponds that resulted in loss of the aboveground vegetation and soils as well as from the loss of tidal influences and inundation altering the formerly suboxic state of the soils to an oxidized state.

The effects of shrimp pond conversion were apparent throughout the soil profile. In their estimations of the emissions arising from land use/land cover change in mangroves, Pendleton et al. (2012) limited losses to C above the soil depth of 1 m. However, the actual field measurements of the study clearly indicates that C losses occurred at depths of >1 m on the soil horizon. This is similar to observations in Malaysia by Ong (1993) who reported the losses at depths as great as 2 m upon conversion of mangroves to shrimp ponds could be as high as 750 Mg C/ha. The losses predicted by Ong (1993) are similar to the losses reported here.

Emissions

Given the role of forests and wetlands as sources and sinks of C and their potential role in climate change mitigation strategies, it is necessary to predict emissions from land-use and land-cover change (GOFC-Gold 2011). One common IPCC (Intergovernmental Panel on Climate Change) protocol for tracking changes in C stocks and predicting emissions from land-cover change in forestry is the stock-change approach (IPCC 2003). Using this approach, we calculated potential emissions that occurred over the life of the abandoned shrimp ponds in this study. We compared them with examples of the emissions that arise from the conversion of tropical upland forests to cattle pasture (Kauffman et al. 2003, Guild et al. 2004). Differences in carbon stocks were converted to emissions using the formula

$$\Delta CLU = \Delta C_{AB} + \Delta C_{BB} + \Delta C_{DW} + \Delta C_{SOC}$$

where CLU means change in carbon stocks (or total C emissions or sequestration) due to land use; ΔC_{AB} , change in aboveground biomass C pool; ΔC_{BB} , change in belowground biomass C pool; ΔC_{DW} , change in dead wood C pool; and ΔC_{SOC} , change in soil organic carbon.

To facilitate comparison among most other assessments, ecosystem C losses are expressed as potential CO₂ emissions, or CO₂ equivalents (CO₂e)—obtained by multiplying C stocks by 3.67, the molecular ratio of CO₂ to C (Fig. 4).

Emissions factors arising from the conversion of mangrove to shrimp ponds would vary by the type of mangrove being converted. Our emissions estimates, based upon our actual measurements, ranged from 2165 Mg CO₂e/ha in low mangrove to 3554 Mg CO₂e/ha in medium mangrove. The emissions calculated as the difference between the mean C stock of mangroves and that of the abandoned shrimp ponds was 2637 Mg CO₂e/ha (Fig. 4). If the mean C stock of the mangroves is representative of the wetlands of Montecristi that have been converted to salt or shrimp ponds, then the cumulative emissions from the 1516 ha that have been converted are 3.8 million Mg CO₂e.

Elsewhere in the tropics the emissions from conversion of upland tropical forests to cattle pasture are comparatively lower (Fig. 4). Using the same approaches as we did for mangroves, the emissions estimates from tropical forest conversion to pastures was 538 Mg CO₂e/ ha in evergreen forests of the Amazon and 230 Mg CO₂e/ha from conversion of primary tropical dry forest in Mexico (Kauffman et al. 2003, 2009). The emissions estimates from forests assume little loss of C from soils (Kauffman et al. 2009). The emissions arising from conversion of tropical evergreen and dry forest to pasture are about 20% and 9% of the predicted emissions arising from the conversion of mangrove to shrimp ponds, respectively. On a comparative basis, the emissions from 1 ha of mangrove converted to shrimp pond is equivalent to the emissions of about 5 ha of tropical evergreen conversion and 11.5 ha of tropical dry forest.

Our estimates are based on empirical measurements of the C stocks of shrimp ponds and mangroves, and are substantially higher than recent estimates given by Donato et al. (2011) and Pendleton et al. (2012). Emissions estimates from Donato et al. (2011) are based upon assumptions of a 50% loss of vegetation biomass and 25% loss of soil C from the top 30 cm to calculate their "low "estimates (411 Mg CO₂e/ha), and a 100% loss of aboveground biomass, 75% loss of the belowground C in the top 30 cm, and 25% loss in deeper layers to 1 m to calculate their "high" estimates (1439 Mg CO₂e/ha). Similarly, Pendleton et al. (2012) provided an emissions estimate of 935 Mg CO₂e/ha based upon the assumption that 63% of the C in vegetation and soils



FIG. 4. Potential C emissions arising from the conversion of tropical ecosystems (Mg CO_2e/ha ; CO_2 equivalents are obtained by multiplying C emissions by 3.67, the molecular ratio of CO_2 to C). Data for the Amazon evergreen rain forest in Brazil are from Kauffman et al. (2009), and data for the Mexican tropical dry forest are from Kauffman et al. (2003). The estimated emissions arising from conversion of mangroves are from Donato et al. (2011; two estimates based on different assumptions) and Pendleton et al. (2012; one mid-point estimate). The emissions for low, medium, and tall mangroves and the mean of all mangroves combined are from the actual measurements reported in this study.

above 1 m in depth would be lost due to mangrove conversion.

The estimates that we provide are based upon the actual measures of C stocks in shrimp ponds and mangroves. These are over two-fold greater than the prediction by Pendleton et al. (2012) and are $\sim 83\%$ greater than the high estimate of Donato et al. (2011). This is significant, as Donato et al. (2011) suggested that worldwide mangrove deforestation generates emissions of 0.02–0.12 Pg C/yr—as much as 10% of the emissions associated with forest conversion—despite accounting for just 0.7% of the tropical forest area. Our emissions estimates from mangroves that are similar to or even lower in C stocks than regions undergoing extensive mangrove conversion, suggest that the global estimates of emissions provided by Donato et al. (2011) may be very conservative.

Mangroves have the relevant characteristics of deep organic-rich soils with exceptionally high C storage. When converted, the C losses are high because large quantities of C formerly stored in suboxic soils are lost, resulting in potentially large greenhouse-gas emissions. Rates of deforestation of mangroves are among the highest of all ecosystems in the tropics (Polidoro et al. 2010). This is at the expense of a large number of ecosystem services and the security of coastal inhabitants. Clearly these factors suggest the value of inclusion of mangroves in climate-change mitigation activities that would maintain the carbon stocks as well as values that mangroves provide to dependent coastal societies as well as to natural ecosystems.

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SUPPLEMENTAL MATERIAL

Appendix A

Equations used to determine biomass of mangrove trees and downed wood at Montecristi National Park (*Ecological Archives* A024-030-A1).

Appendix **B**

Plot locations (latitude and longitude of the first plot of each site), soil depth, soil carbon and nitrogen concentration, bulk density and the soil C and N stocks of mangroves and abandoned shrimp ponds in and around Montecristi National Park (*Ecological Archives* A024-030-A2).