LETTER

Predicting Global Patterns in Mangrove Forest Biomass

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Abstract

Understanding spatial variation in carbon storage in natural habitats is critical for climate change mitigation efforts such as REDD. Terrestrial forests are being mapped with increasing accuracy, but the distribution of "blue carbon" in marine ecosystems remains poorly understood. We reviewed the literature to obtain field data on carbon storage and fluxes in mangroves world-wide. Using this material we developed a climate-based model for potential mangrove above-ground biomass (AGB) with almost four times the explanatory power of the only previous published model. From this model, we present the first ever global map of potential mangrove AGB and estimate a total global mangrove AGB of 2.83 Pg, with an average of 184.8 t ha^{-1}. Data on other carbon stocks and fluxes confirm the importance of mangroves in carbon accounting. The map highlights the high variability in mangrove AGB and indicates areas that should be prioritised for mangrove conservation and restoration.

Introduction

Deforestation, particularly in tropical regions, is the second largest source of anthropogenic CO_2 emissions after fossil fuels, contributing 12–20% of the total (IPCC 2007; van der Werf *et al.* 2009). Understanding spatial variation in forest biomass and productivity is therefore crucial for refining global climate models and developing policy responses, including REDD and similar mitigation efforts (Nepstad *et al.* 2011; Grabowski & Chazdon 2012).

There are growing efforts to more accurately map carbon stocks and fluxes at global scales (Saatchi *et al.* 2011; Baccini *et al.* 2012), but mangroves have largely been ignored in these syntheses due to their small spatial extent and the mapping challenges they present. Despite this small extent, field studies have shown mangroves to have high above-ground biomass, productivity (e.g., Putz & Chan 1986; Matsui 1998; Alongi *et al.* 2004), soil carbon (Donato *et al.* 2011), below-ground to above-ground biomass ratios (Komiyama *et al.* 2008; Lovelock 2008), and high rates of carbon sequestration (Mcleod *et al.* 2011; Alongi 2012; Breithaupt *et al.* 2012).

Mangroves are also highly threatened. A third of the world's mangroves have likely been lost over the last 50 years largely through conversion for aquaculture or agriculture (Alongi 2002). Annual deforestation rates were estimated at ~0.7% from 2000–2005 (Spalding *et al.* 2010), similar to or higher than those for tropical forests and three to five times greater than mean global rates of forest loss (FAO 2006). Rapid loss rates, combined with high carbon values means that, despite their small extent, mangroves may contribute 10% of total carbon emissions from deforestation (Donato *et al.* 2011).

Some earlier studies attempted to derive estimates of global average carbon stocks and fluxes in mangrove forests (e.g., Alongi 2009; Donato *et al.* 2011). Two of these incorporated a model of spatial variation, using a simple linear relationship of above-ground biomass with latitude (Twilley *et al.* 1992; Siikamäki *et al.* 2012). In this paper, we synthesize the findings from a new review of mangrove biomass and productivity from 95 field studies. Using some of these data, we develop a climate-based model for estimating mangrove above-ground biomass. By linking this to global data on climate and mangrove distribution, we present the first ever global map of predicted mangrove above-ground biomass.

Methods

Literature search

We used Google Scholar and Web of Science to find studies giving data on mangrove carbon stocks and fluxes. Initial search terms were "mangrove" plus "carbon," "carbon storage," "carbon sequestration," "carbon fixation," "biomass," "productivity," and "litter fall." The search was expanded by following references from the initial result set. We found studies giving measures of above-ground biomass, below-ground (root) biomass, soil carbon, above-ground primary productivity, litterfall, and soil carbon accumulation rates. For soil carbon accumulation rate we found very little data, so no further analysis was carried out. We determined sampling site locations using Google Earth. Studies were only included if the location could be determined to within 0.01° of latitude and longitude, using coordinates, published maps, or place names. Studies from regenerating or planted mangroves were excluded from the analysis where stands were less than 10 years old.

We also excluded remote sensing studies which estimate biomass from proxies such as canopy height, measured using Shuttle Radar Topography Mission or Geoscience Laser Altimeter System data. Such approaches are proving highly valuable for capturing local scale variance in biomass, but they also introduce new uncertainties, both around the estimation of canopy height, and in the allometric equations used to derive biomass estimates (Fatoyinbo & Simard 2013). These uncertainties are much larger than those from field studies, which tend to use locally derived species-specific allometric equations and measure trunk diameter at breast height, a better predictor of biomass than canopy height (Chave *et al.* 2005).

Climate model of above-ground biomass

Although we were able to gather considerable data for many variables, only the dataset for above-ground biomass (AGB) proved sufficiently large to develop a robust model. We briefly investigated the latitude-based model developed by Twilley *et al.* (1992) and recently used to develop a global biomass estimate (Siikamäki *et al.* 2012). However, this model explained little of the variation observed in our sample (see section "Results") so we attempted to develop a model based on climate. For each location where we had AGB measures, we extracted bioclimatic data from the WorldClim Bioclim 30 arc-second dataset (http://www.worldclim.org/bioclim), a global interpolated dataset of 19 bioclimatic variables, derived from monthly temperature and rainfall (Hijmans *et al.* 2005).

To prevent clustered sampling points having disproportionate influence, we merged points within 10 km of each other and used their mean AGB values. From the original 102 locations for AGB, this left us with 52 points for use in the model. Bioclim is a terrestrial dataset, so where mangroves fell in areas classified as water, the climate values were taken from the nearest point with data.

Many of the variables in the Bioclim dataset are highly correlated, making it necessary to choose a subset for use in the model. Working on the assumption that mangrove biomass will be affected by temperature and precipitation, we chose two sets of variables to represent these (Table 1). The first set used an annual summary measure (mean temperature and total precipitation) with a measure of the variation (standard deviation of monthly temperature and coefficient of variation of monthly precipitation) to give an overall representation of climate and seasonality. The second set assumed that mangrove biomass might be limited by extremes of heat, cold, and drought, and therefore used the mean temperature of the warmest and coldest quarters and the precipitation of the wettest and driest quarters. We used quarterly rather than monthly measures as mangroves are large plants with adaptations to dry conditions so seem unlikely to be affected by monthly fluctuations. We fitted two linear models with AGB as a response variable and each of the two sets of climatic variables as predictors. We also experimented with a model including climate variables and latitude. The models were compared using Akaike information criterion (AIC), which gives an indication of which model gives the most information for the least complexity. We used bootstrap resampling with 1,000 runs to generate confidence intervals for the predicted biomass measures. Models were fitted using R version 2.14 (R Development Core Team 2011).

Mapping

We applied our best model to the global layers in Bioclim and the mangrove map developed by Spalding *et al.* (2010) to construct a worldwide map of potential mangrove AGB. To avoid extrapolating beyond the conditions used to build the models, we set any climate values above (or below) the range found in our study sites to the maximum (or minimum) of that range. The predicted AGB

Table 1 The two sets of climate variables used for modeling (see www.worldclim.org/bioclim)

Set 1: averages and seasonalities		Set 2: extremes	
Variable	Name	Variable	Name
BIO1	Annual mean temperature (°C)	BIO10	Mean temperature of warmest quarter (°C)
BIO4	Temperature seasonality: S.D. of monthly mean temperature.	BIO11	Mean temperature of coldest quarter (°C)
BIO12	Annual precipitation (mm)	BIO16	Precipitation of wettest quarter (mm)
BIO15	Precipitation seasonality: CV of monthly precipitation	BIO17	Precipitation of driest quarter (mm)

map layer was then used to calculate global, regional, and national summary statistics.

Other measures

We summarized data on other carbon stocks and fluxes for comparison to previous estimates. For below-ground (root) biomass (BGB), we derived an allometric relationship with AGB, using data from field sites where we had measures of both variables. We used this to add an indirect estimate of BGB to our spatial model.

Results

The literature search produced 95 studies (Table S1), with 337 values for carbon storage and productivity proxies (Table 2) from 242 different locations. These represent data from 35 countries, covering most of the latitudinal range of mangroves (from 28°N to 37°S, Figure 1), including continental and island locations, and climate settings from temperate estuaries to desert margins to wet tropical regions.

Latitude model

Applying Twilley *et al.*'s (1992) latitude-based relationship (Equation (1)), to our larger data set ($n = 52$) only explained 7.6% of worldwide variation in AGB ($R^2 = 0.076$). Reparameterizing this latitudinal model using our data gave a new linear regression (Equation (2)), with a much improved fit (decrease in AIC of 3.68), and explaining almost twice the variance (13.9%).

(**from Twilley** *et al.* 1992):

$$\text{AGB}(\text{t ha}^{-1}) = -7.291\ \text{Latitude(decimal degrees)} + 298.5 \qquad (1)$$

(**fitted to our dataset**):

$$\text{AGB}(\text{t ha}^{-1}) = -4.617\ \text{Latitude(decimal degrees)} + 239.9 \qquad (2)$$

Climate model

Both our climate models, one based on annual extremes and the other based on mean and variation in temperature and precipitation, were better supported than the fitted latitude model (ΔAIC = 2.39 and 1.27, respectively) and the original Twilley *et al.* relationship (ΔAIC = 6.09 and 4.96), and explained 26.7% and 25.1% of global variation in AGB respectively (i.e., an almost fourfold increase on the explanatory power of Twilley *et al.*'s original relationship). The climate variables in set 2 marginally outperformed those in set 1 (ΔAIC = 1.13, with an increase in R^2 of 1.6%), so we used this model (Equation (3)) to develop our maps.

$$\text{AGB}\left(\text{t ha}^{-1}\right) = 0.295\text{BIO10} + 0.658\text{BIO11} + 0.0234\text{BIO16} + 0.195\text{BIO17} - 120.3. \qquad (3)$$

(BIO10 = mean temperature of warmest quarter, BIO11 = mean temperature of coldest quarter, BIO16 = precipitation of wettest quarter, and BIO17 = Precipitation of driest quarter. See Table 1 for further explanation.)

This equation indicates that biomass is higher in areas with higher temperatures, especially in the coldest quarter. Areas with higher rainfall, especially in the driest quarter, also have higher biomass. Adding latitude to the model slightly increased AIC (ΔAIC = 0.80), indicating that it did not add any additional information. See Figure S1 for plots of the individual predictors against our dataset.

The global patterns of AGB predicted by the model are shown on the map in Figure 2.

Global, regional, and national totals

The model predicts a total global AGB in the world's mangroves of 2.83 Pg (95% confidence interval 2.18–3.40 Pg), and a global mean AGB of 184.8 t ha^{-1} (95% CI 142.1–222.0 t ha^{-1}). Southeast Asia accounts for almost half of total global AGB: this region not only has the largest area of mangroves, but also has the highest mean AGB per unit area—nearly double that of the Middle East

Table 2 The final data sets from the literature search. Figures in brackets are before points within 10 km of one another were merged. Summary statistics are taken from the merged datasets

	Variable	n	Mean	Median	Standard deviation
Stocks	Above-ground biomass (t ha^{-1})	52 (102)	165.52	142.78	121.30
	Below-ground biomass (t ha^{-1})	30 (55)	78.63	38.62	94.63
	Soil carbon (t C ha^{-1})	21 (40)	446.91	444.96	175.44
Fluxes	Above-ground net primary productivity (t biomass ha^{-1} yr^{-1})	37 (56)	29.25	18.78	30.12
	Litter fall (t biomass ha^{-1} yr^{-1})	46 (84)	9.64	9.84	4.13
	Soil C accumulation (t C ha^{-1} yr^{-1})	6 (17)	2.04	1.54	1.53

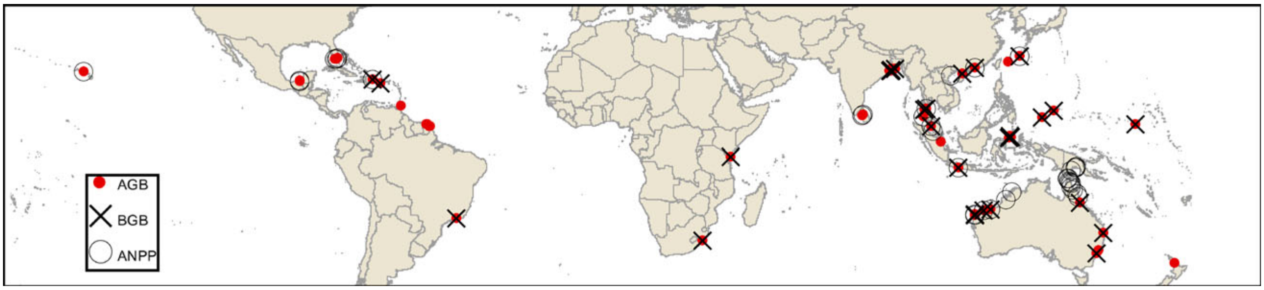

Figure 1 Global map of mangroves showing the locations where data were obtained for one or more measures of carbon stocks and fluxes.

(Table 3). Table 4 shows national statistics for the 10 countries with the largest mangrove AGB.

Below-ground biomass

We developed an allometric relationship between AGB and BGB (Equation (4)), from sites where we had data for both variables ($n = 41$, adjusted $R^2 = 0.712$, $F_{1,39} = 100$, $P < 0.001$).

$$\mathrm{BGB}\left(\mathrm{t\ ha}^{-1}\right) = 0.073\mathrm{AGB}^{1.32}\left(\mathrm{t\ ha}^{-1}\right). \quad (4)$$

Applying this equation to our modeled AGB layer gave a global total BGB of 1.11 Pg (95% CI 0.74–1.64 Pg), giving a total combined biomass (AGB plus BGB) of 3.95 Pg. This gives a global mean BGB:AGB ratio of 0.39, which, when compared to a mean ratio of 0.28 for tropical terrestrial forests (Saatchi *et al.* 2011), supports earlier work showing a high proportion of below-ground biomass in mangroves (Komiyama *et al.* 2008).

Other biomass measures

Our datasets for other mangrove carbon stocks and fluxes were too small for modeling with climate datasets, but they are still an important compilation permitting some limited assessment, as set out in Table 2. For more discussion of these results see Supplementary Information.

Discussion

Our climate-driven model provides an almost fourfold increase in explanatory power compared to the only other published relationship exploring spatial variation in mangrove biomass (Twilley *et al.* 1992). Using this model, our global estimate of AGB is lower than both this original estimate and a more recent update (Siikamäki *et al.* 2012). Nonetheless, our models imply that mangroves still host 1.4% of global tropical forest AGB and 1.6% of the total tropical forest biomass (AGB and BGB) of 247 Pg estimated by Saatchi *et al.*, despite occupying only 0.6% of tropical forest area (using the 10% canopy cover definition).

By contrast, our AGB estimates are larger than those from recent remote sensing studies. Fatoyinbo & Simard (2013) estimate total mangrove biomass for Africa to be 301.7 million tonnes compared to 502.6 million tonnes from our model. Part of this can be explained by differences in the baseline map of mangrove extent (their study maps 25,960 km^2 compared to our estimate of 30,751 km^2). Further differences are probably due to degraded mangrove areas: both studies produce similar estimates for Gabon, which has some of the most pristine mangrove habitat in Africa (23.89 million tonnes with our model, compared to 23.84 million tonnes from Fatoyinbo and Simard), but in Nigeria, where mangroves have been extensively degraded through pollution and harvesting,

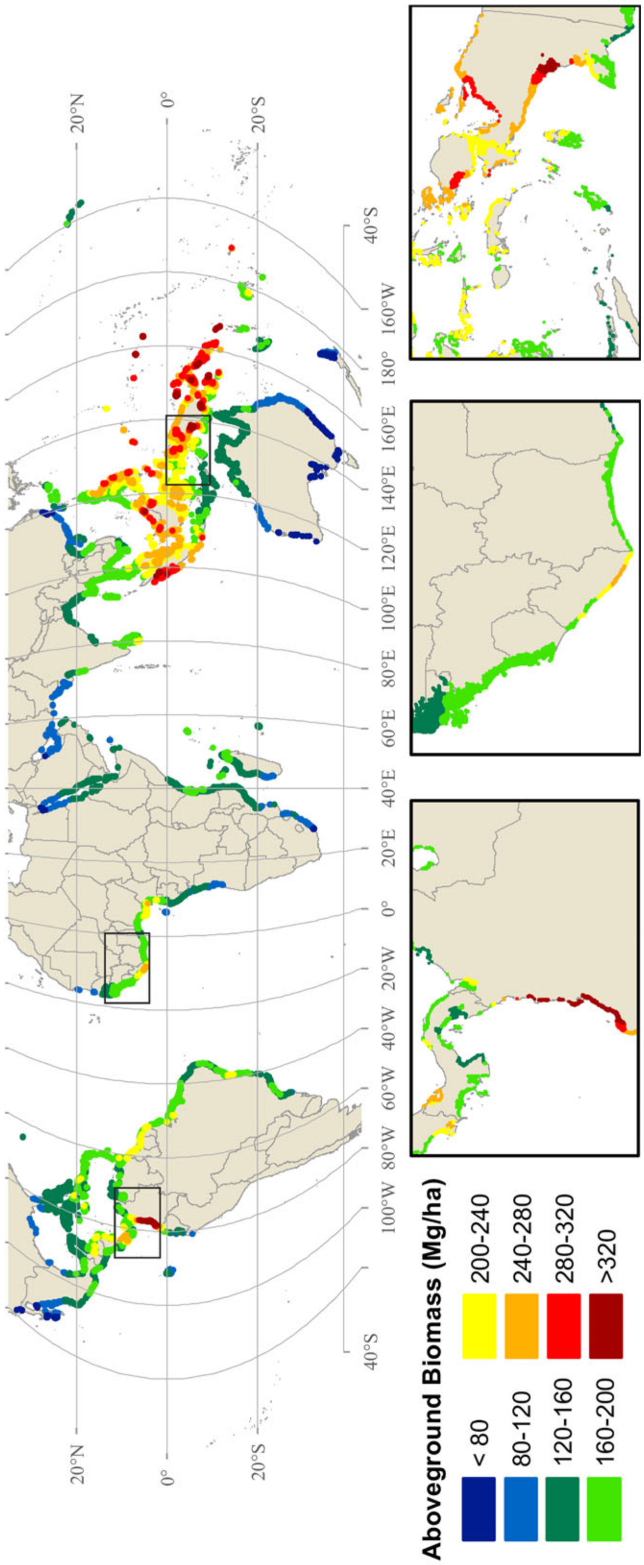

Figure 2 Global mangrove map showing modeled patterns of above-ground biomass per unit area.

their biomass estimate is only 60% of ours (94.8 million tonnes vs. 152.0 million tonnes).

When it becomes available, a global biomass estimate from remote-sensing surveys will provide a valuable alternative to our modeled approach, offering real data at much higher resolution, capable of showing patterns of variance even within individual mangrove tracts, and with the possibility of tracking change. Even so, our approach will remain useful in helping to understand drivers of variance, and in enabling some idea of the potential carbon values that might be returned following restoration or recovery of degraded systems. It also provides proof-of-concept for modeling methods that might be adapted, using other drivers, to map ecosystem services which cannot be easily derived from remote sensing, including carbon stocks and fluxes in other habitats, or measures of value for fisheries or coastal protection.

Spatial variability

The most striking feature of our map of AGB is the high level of variation. Low AGB areas (below 80 t ha^{-1}) are found at the limits of mangrove distribution where the key climatic variable is typically cold temperature, but may also include aridity (e.g., in western Mexico and in the Middle East). Mangrove forests with high AGB are more variable in their distribution, but our highest values (above 280 t ha^{-1}) are typically associated with tropical areas with year-round high rainfall. These patterns appear to follow trends in AGB for terrestrial forests (Saatchi *et al*. 2011; Baccini *et al*. 2012).

Limitations

Fine-scale variation and zonation in forest structure is not captured in our model. However, we believe that both the field data and our aggregation of clustered sites have helped generate representative mean estimates at landscape scales.

As discussed above, the model also does not account for anthropogenic alteration or degradation. Overharvesting, disease, pollution, and other impacts can alter forest structure, and hence impact biomass and productivity. While some field studies may include sites with some degree of degradation, there is likely to be a sampling bias toward relatively healthy forests. In areas where mangroves have been extensively degraded, our map therefore represents potential biomass, rather than existing biomass.

The largest gaps in our input data for the model were from Central and West Africa and the Pacific coast of the Americas. While this highlights areas for research attention, the species composition of mangrove communities in these regions is very similar to that found elsewhere, so we believe that our model remains relatively robust even in these areas.

Estimates of global biomass will of course be influenced by the accuracy of the base map of mangroves. We used the *World Atlas of Mangroves* dataset which was largely built up from 1999–2003 Landsat images, using a variety of image-processing techniques and with considerable expert review (Spalding *et al*. 2010). The global map produced by Giri *et al*. (2011), and the map of African mangroves developed by Fatoyinbo & Simard (2013) use essentially the same Landsat imagery, with less expert review, but more systematic processing. Each map has somewhat different estimates of mangrove cover, and there has been no detailed comparison of these to assess accuracy. In all cases it is worth noting that the images are now 10–14 years out of date, and rates of loss suggest that global biomass would have declined substantially in that time frame.

Policy implications

Our map provides a valuable tool for assessing carbon stocks and highlighting priority areas for conservation and restoration interventions. These include:

(1) Countries with high total mangrove biomass such as Indonesia, Nigeria and Brazil, where effectively implemented national policies could make an important contribution to global carbon fluxes.
(2) Countries with high average biomass, where investment in mangrove conservation could yield high returns per unit area.
(3) Countries where mangroves make up a large proportion of total forest, including Small Island Developing States (SIDS) such as Cuba and the Solomon Islands, where awareness of the high-carbon values of mangroves could foster engagement with policy and market-based instruments for forest conservation.
(4) Countries with high-mangrove biomass loss rates, which offer the greatest potential for interventions to slow emissions. Indonesia is the prime example, with high rates of mangrove forest loss and high average AGB (FAO 2007).
(5) Countries where mangrove restoration will yield high-carbon benefits. This could be particularly valuable in locations which have lost much of their mangroves such as Java, Thailand, the Philippines, and southern China (Spalding *et al.* 2010).

Policy and market-based approaches are likely to be critical in increasing efforts to reduce mangrove loss and to stimulate restoration (Siikamäki *et al.* 2012). While funding mechanisms through schemes such as REDD still

Table 3 Total AGB and mean AGB per unit area for different regions. Regions are those used by Spalding *et al*. (2010)

Region	AGB (t)	Upper 95% confidence interval	Lower 95% confidence interval	Mangrove area (ha)	Mean ABG (t ha^{-1})
Eastern and Southern Africa	143,328,000	189,446,000	106,207,000	1,050,958	136.4
Middle East	14,746,000	22,258,000	7,564,000	133,585	110.4
South Asia	136,602,000	173,379,000	79,701,000	1,001,443	136.4
Southeast Asia	1,131,563,000	1,495,693,000	810,748,000	4,901,429	230.9
East Asia	2,535,000	3,328,000	1,368,000	23,642	107.2
Australia and New Zealand	87,510,000	109,993,000	67,911,000	658,247	132.9
Pacific Islands	133,465,000	179,902,000	83,623,000	572,099	233.3
North and Central America and the Caribbean	356,290,000	443,465,000	277,714,000	2,452,775	145.3
South America	465,905,000	561,794,000	349,145,000	2,509,463	185.7
West and Central Africa	357,443,000	455,389,000	235,014,000	2,010,453	177.8
Global Total	2,829,387,000	3,400,109,000	2,176,178,000	15,314,094	184.8

Table 4 Total AGB and mean AGB per unit area for the 10 countries with the largest total mangrove AGB. See Table 2 for a more complete list of countries

Country	AGB (t)	Upper 95% confidence interval	Lower 95% Lowerconfidence interval	Area (ha)	Country mean (t ha^{-1})
Indonesia	729,075,000	984,785,000	451,694,000	2,986,496	244.1
Brazil	227,460,000	291,042,000	166,694,000	1,347,998	168.7
Malaysia	179,186,000	244,416,000	114,869,000	709,661	252.5
Nigeria	152,010,000	184,828,000	107,497,000	778,944	195.1
Mexico	134,907,000	172,710,000	103,236,000	964,438	139.9
Colombia	103,870,000	142,423,000	66,624,000	410,152	253.2
Papua New Guinea	98,684,000	132,809,000	61,891,000	418,611	235.7
Burma	89,001,000	127,313,000	34,889,000	514,261	173.1
Australia	85,489,000	107,631,000	66,226,000	632,164	135.2
Cuba	69,628,000	95,092,000	52,267,000	495,975	140.4
Global total	2,829,387,000	3,400,109,000	2,176,178,000	15,314,106	184.8

face significant challenges, other approaches such as offset markets are already beginning to receive some interest and investment (Giraud & Hemerick 2012). Critical to the development of stronger policy incentives will be to move beyond the global averaging of ecosystem service values to spatially explicit measures. Our modeling approach provides a simple measure for one carbon stock, and, with better data, might be similarly developed for other stocks and fluxes, and for other ecosystems. Higher resolution approaches will certainly prove more valuable for site level assessments, but global and regional maps of variance remain important for influencing large-scale policy and investment.

Beyond carbon storage, mangroves deliver a host of other ecosystem services, including coastal protection, fisheries, timber, water purification and biodiversity (e.g., Sathirathai & Barbier 2001; Gunawardena & Rowan 2005). Increased investments to secure individual ecosystem services are therefore likely to yield multiple additional economic and social benefits. Similarly, improvements in understanding the value and drivers of other ecosystem services may further bolster efforts to manage, maintain, or restore mangroves. The mapping of patterns in such values has the potential to greatly help direct where climate, development and conservation resources can be spent to best effect.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Disclaimer: Supplementary materials have been peer-reviewed but not copyedited. The following supplementary material is available for this article:

Figure S1 Plots of the 52 AGB data points against the climate variables used in the final model.

Figure S2 Plot of the 52 AGB observed values against the values predicted by the model for those locations, with a 1:1 line.

Table S1 References for biomass and flux data found by the literature search.

Table S2 AGB and BGB mean and total by country, sorted by total AGB, for all countries with >5000 ha of mangroves.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1755–263X.2008.00002.x (This link will take you to the article abstract).

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