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Spatial variability of mangrove primary productivity in the neotropics

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Abstract. Mangroves are considered one of the most productive ecosystems in the world with significant contributions as carbon sinks in the biosphere. Yet few attempts have been made to assess global patterns in mangrove net primary productivity, except for a few assumptions relating litterfall rates to variation in latitude. We combined geophysical and climatic variables to predict mangrove litterfall rates at continental scale. On a per-area basis, carbon flux in litterfall in the neotropics is estimated at 5 MgC·ha⁻¹·yr⁻¹, between 20% and 50% higher than previous estimates. Annual carbon fixed in mangrove litterfall in the neotropics is estimated at 11.5 TgC, which suggests that current global litterfall estimates extrapolated from mean reference values may have been underestimated by at least 5%. About 5.8 TgC of this total carbon fixed in the neotropics is exported to estuaries and coastal oceans, which is nearly 30% of global carbon export by tides. We provide the first attempt to quantify and map the spatial variability of carbon fixed in litterfall in mangrove forests at continental scale in response to geophysical and climatic environmental drivers. Our results strengthen the global carbon budget for coastal wetlands, providing blue carbon scientists and coastal policy makers with a more accurate representation of the potential of mangroves to offset carbon dioxide emissions.

Key words: carbon budgets; climate change; litterfall; macroecology; mangrove primary production; neotropics; spatial variability.

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INTRODUCTION

Mangrove forests have global distribution of 81,848 km² (Hamilton and Casey 2016), which is a fraction of the total extent of tropical forests (Giri et al. 2011). However, these coastal forested wetlands are among the most productive ecosystems in the world, playing a major role as sinks in the global carbon (C) cycle (Twilley et al. 1992,

Bouillon et al. 2008). Global patterns of mangrove net primary productivity have been associated with variation in coastal geomorphology (relative contribution of river discharge, tidal flushing, and wave energy) and climatic regimes (temperature, precipitation, and evapotranspiration; Lugo and Snedaker 1974, Thom 1982, Twilley 1995). In general, mangroves occurring in coastal morphologies with higher temperatures,

tidal range, and riverine inputs (freshwater and nutrient discharge) are more productive than mangroves exposed to harsh environments (e.g., low temperatures, seasonal droughts, and hypersalinity; Fosberg 1961, Pool et al. 1975, Twilley et al. 1986, Schaeffer-Novelli et al. 1990). Net primary productivity also varies across different ecological types of mangroves as a function of hydroperiod (flooding frequency, duration, and depth; Lugo and Snedaker 1974). These differences occur primarily due to nutrient availability, presence of continuous freshwater sources that reduce soil salinity, and hydroperiod that promotes benign coastal environmental settings (Twilley et al. 2017).

Mangrove total net primary production includes wood production and litterfall as aboveground production together with belowground (or roots) production (Twilley et al. 2017). Simultaneous measurement of both above- and belowground components of net production is scarce in the literature (Bouillon et al. 2008, Castañeda-Moya et al. 2013, Twilley et al. 2017). Although accounting for only 32% of mangrove total net primary production (Bouillon et al. 2008), litterfall is the most common metric used to compare mangrove net primary productivity across sites (Kristensen et al. 2008, Castañeda-Moya et al. 2013, Twilley et al. 2017). This is likely due to the relative feasibility in assessing this component in contrast to methodological constraints associated with wood and root productivity (Kristensen et al. 2008). While most studies have investigated site-specific influence of environmental variables on mangrove litterfall, only few attempts have been made at global scales, generally showing litterfall rates as negative correlation with latitude (Twilley et al. 1992, Saenger and Snedaker 1993, Bouillon et al. 2008). However, these latitude-based models do not account for the variability in climate regimes and geophysical conditions with coastal morphology that can vary with latitude. Given the global significance of mangroves to C cycle, robust global estimates of C production require methods to scale these processes across diverse climatic and coastal morphology drivers associated with coastal environmental settings where mangrove ecosystems occur (Clarke 2014, Rivera-Monroy et al. 2017).

The use of global climatic gridded data as environmental predictors of mangrove structural

and functional attributes is a powerful alternative to latitude-based models. For instance, precipitation and air temperatures can predict global patterns to explain mangrove distribution, species composition, and abundance (Record et al. 2013, Osland et al. 2017b), in addition to aboveground biomass (Hutchison et al. 2014), and soil carbon stocks (Jardine and Siikamäki 2014). However, combining climatic variables with geophysical forces such as tides and river discharge into predictive models is a relatively new approach in mangrove macroecology, but has shown to improve global mangrove C estimates in aboveground biomass and soils (Rovai et al. 2016, 2018). Here, we used the coastal environmental setting framework (Twilley et al. 2018) to ask whether continental variation in mangrove litterfall is controlled by a combination of geophysical and climatic variables. To our knowledge, no study to this date has attempted to estimate mangrove litterfall at global scales considering the integrated effects of geophysical and climatic drivers. We hypothesized that, at continental scale, mangrove litterfall increases with river discharge, tidal amplitude, precipitation, and temperature, and decreases with potential evapotranspiration (PET). To test our hypothesis, we used the neotropical biogeographic province spanning 60° in latitude and 90° in longitude, which accounts for approximately 30% of the world's mangrove coverage (Hamilton and Casey 2016). In addition, the neotropics include the global diversity of coastal environmental settings where mangroves develop, including deltas, estuaries, lagoons, carbonate, and arctic coastline types (Twilley et al. 2018). Moreover, the neotropics shelter the two most cosmopolitan mangrove genera, *Rhizophora* spp. and *Avicennia* spp., which are present in every continent where mangroves occur. Altogether, the diversity of biogeographic, geomorphologic, and climatic properties makes the neotropics an excellent observatory to address macroecological questions. Our approach was to model mangrove litterfall across the neotropics using distinct coastal geomorphology driving forces (river discharge, tidal range) and climatic regimes (temperature, precipitation, evapotranspiration) as environmental predictors. To achieve this goal, we built a comprehensive dataset on mangrove litterfall studies representing

the global diversity of environmental settings and climatic regimes where mangroves thrive.

MATERIALS AND METHODS

We compiled a dataset from published and unpublished studies based on litterfall collection for the neotropics (see Appendix S1 for reference list). We performed searches using the term “mangrove” and “manglar” as keywords in Web of Science, Scopus, and BDTD databases (<http://bdt.d.ibict.br>). We also performed searches in the CAPES Thesis Database (<http://catalogodeteses.capes.gov.br>) using the term “manguezal” (mangrove in Portuguese). After removing duplicate references, we used the following keywords in English, Portuguese, and Spanish languages: “litterfall”, “litter production”, “litter”, “primary production”, “productivity”, “NPP”, and “net primary productivity”. We also linked these keywords with each country (or territory) in the neotropics where mangroves are present. References not available online were requested directly to authors using e-mail whenever possible or acquired through university interlibrary systems. We excluded from our analysis sites that were described in the original study as impacted by anthropogenic activities, plantations (including planting and replanting for allegedly restoration purposes), and young (e.g., developing) mangrove forests to avoid litterfall under- or overestimation at any specific location. However, sites subject to natural disturbances such as tropical cyclones, freezing temperatures, and hypersalinity were considered, as they represent the natural variation of environmental conditions to which mangroves are adapted. We classified each site resulting from our literature survey into different types of coastal environmental settings, including deltas, estuaries, lagoons, composite river/wave-dominated, and carbonate peat-dominated coastlines (see Rovai et al. 2018 and references therein for details). We used pairwise Wilcoxon rank-sum test to assess differences in litterfall among these distinct coastal environmental settings.

The mangrove surface area coverage used to model litterfall across the neotropics was obtained from a global distribution map of mangroves derived from remote sensing imagery (Hamilton and Casey 2016). We aggregated sites

by calculating median values within each cell in a 0.25° spatial resolution grid containing litterfall values in an attempt to balance the amount of available data between response and explanatory variables (Blackburn and Gaston 2002). In addition, this resolution is spatially representative of most coastal environmental setting domains we based our modeling framework. Our final dataset comprised 71 litterfall values, which was the sample size used in our regression analyses. We extracted geophysical and climatic environmental variables from global gridded datasets for each degree cell containing mangrove litterfall data. Minimum precipitation of the driest month (P_{\min} , mm/yr) and minimum temperature of the coldest month (T_{\min} , °C) were obtained from Bioclim (Hijmans et al. 2005). Potential evapotranspiration (mm/yr) was derived from Moderate Resolution Imaging Spectroradiometer (MODIS; Mu et al. 2011). Global tidal range was acquired from the difference between mean high spring tides and mean low spring tides, where the highest value of the sum of the two major tidal constituents (semidiurnal or diurnal amplitudes) was further multiplied by two to obtain the tidal range (TR, cm; Carrère et al. 2012). River discharge (m^3/s) was retrieved from the Global Runoff Data Centre (Fekete et al. 2002). We pre-selected these variables as potential predictors of mangrove litterfall considering their ecological significance to mangrove structural and functional attributes (Thom 1982, Woodroffe 1992, Twilley 1995, Rovai et al. 2016, 2018).

Environmental variables were previously tested for autocorrelation and multicollinearity using Spearman's correlation rank and variance inflation factor (VIF), respectively. We used multiple regression (ordinary least squares) to evaluate which set of environmental variables had significant effects on the variability of litterfall across the neotropics. We used Akaike information criterion (AIC) to select among the candidate models generated during the automated model selection procedure (see Barton 2018 for details) the one that best described our data. We used ANOVA to assess the significance of model's terms to mangrove litterfall variability. Model residues were checked for normality using Shapiro's test, and lack of fit was verified using pure error analysis. The relative importance of each predictor to litterfall variability was assessed

based on coefficient of determination (R^2) partition (Grömping 2006). We used k -fold ($k = 10$) cross-validation technique to verify the predictive accuracy of our model outputs by splitting our data into k random sample portions and keeping one of the k subsets as test data during each iteration (Maindonald and Braun 2015). To calculate the C density in annual mangrove litterfall, we multiplied the predicted litterfall value within each grid cell by the mangrove surface coverage area of that same cell using the global distribution map of mangroves provided by Hamilton and Casey (2016). To obtain the total annual C fixed in litterfall, the values from every grid cell in the neotropics were summed up. For comparison purposes, we used global estimates provided by Bouillon et al. (2008) but adjusted to an updated global mangrove surface area of 81,848 km² (Hamilton and Casey 2016) and to a C conversion factor of 0.5 (Hamilton and Friess 2018). Statistical analyses were performed in R (R Core Team 2018) using untransformed data.

RESULTS

The dataset used in our analysis contains litterfall data for 329 sites retrieved from 88 studies, encompassing different coastal environmental settings and covering 47% of the countries and territories containing mangroves in the neotropics (Fig. 1). Overall, mean litterfall rates were higher in river-dominated systems (particularly in deltaic coastlines; 11.5 Mg·ha⁻¹·yr⁻¹), and the lowest values were reported for carbonate settings (<2 Mg·ha⁻¹·yr⁻¹; Fig. 2). The similarity between composite river-wave-dominated settings and river-dominated systems may be due to the reduced number of observations in the former coastal setting.

None of the pre-selected environmental variables exhibited correlation problems, with a maximum linear correlation coefficient of 0.49 (TR ~ RD), and VIF values ranging from 1.04 (RD) to 1.22 (PET), indicating no multicollinearity. Thus, all environmental variables were included in a global model for the regression analysis. The automated model selection generated a set of 76 possible model combinations (Appendix S1: Table S1). The best-fit model included the interaction term $P_{\min}:T_{\min}$ and TR, explaining 25% of

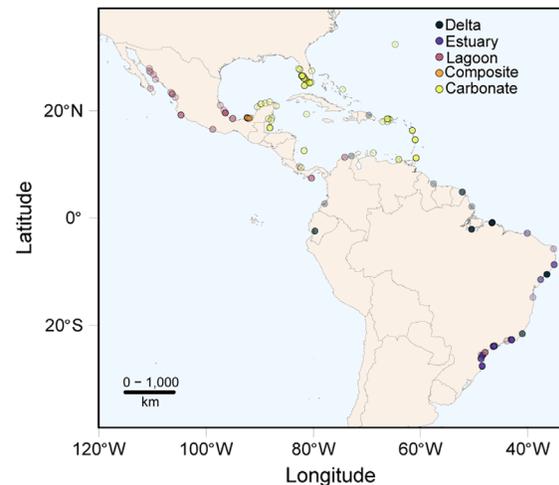


Fig. 1. Distribution of mangrove litterfall data across the neotropics ($N = 329$ sites). Symbols' colors illustrate distinct coastal environmental settings. Transparency was added to facilitate visualization of overlapping sites.

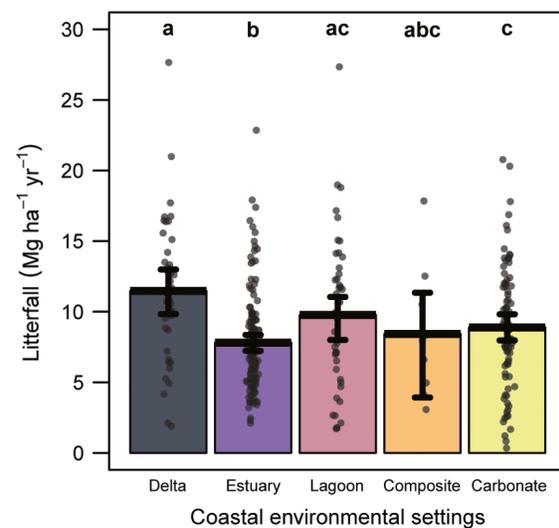


Fig. 2. Variability of mangrove litterfall values in the neotropics ($N = 329$). Bars show group means ($\pm 95\%$ confidence interval) and lower-case letters difference among groups ($P < 0.05$). Bars' colors and group names denote different coastal environmental settings as shown in Fig. 1.

the mangrove litterfall variability across the neotropics (adjusted $R^2 = 0.2496$, $df = 66$, $F = 6.82$, $P = 0.0001$). Model's terms were significant to explain the variability in mangrove litterfall across

the neotropics (Appendix S1: Table S2), and residues were normally distributed (P -value = 0.7). The interaction $P_{\min}:T_{\min}$ explained most of the variability (40.2%), followed by T_{\min} (25.5%), TR (22.5%), and P_{\min} (11.8%). Thus, the equation we used to predict mangrove litterfall across the neotropics was

$$\begin{aligned} \text{Litterfall}(\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}) \\ = 11.704 + (0.010\text{TR}) + (-0.156P_{\min}) \\ + (-0.192T_{\min}) + [0.009(P_{\min}T_{\min})]. \end{aligned} \quad (1)$$

Predicted litterfall values ranged from 1.66 to 28.81 $\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ with a mean of 10.25 $\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fig. 3). Cross-validation showed that our model predicts reasonably well when fit to new data. Using a biomass-to-C conversion factor of 0.5 (see Hamilton and Friess 2018, for details), predicted mean litterfall corresponds to 5 $\text{MgC} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. The C flux in litterfall in the neotropics is estimated at 11.5 TgC/yr . Low values were predicted for areas with low rainfall, frosts, or no river input, such as Louisiana (USA), Florida (USA), and Caribbean Islands (i.e., Puerto Rico), whereas high litterfall rates were associated with coastlines subjected to higher temperature and rainfall regimes, increased tidal exchange, and high riverine discharge, such as near the San Juan River Delta (Colombia), Orinoco Delta (Venezuela), Essequibo River (Guyana), and Amazon Delta (Brazil; Fig. 3).

DISCUSSION

Here, we provide a statistical-based model that accounts for continental-scale variability in mangrove litterfall in response to climatic and geophysical variables combined. Our results advance the current understating of mangrove litterfall variability across latitudinal and longitudinal gradients as a function of geophysical forces, considering previous studies did not account for factors responsible for large-scale variability. Instead, correlations were usually performed using absolute variation in latitude degrees as a predictor of mangrove net primary productivity (Twilley et al. 1992, Saenger and Snedaker 1993, Bouillon et al. 2008). Although latitude can indirectly include geophysical forces,

local environmental drivers within latitude cannot be discerned or weighted in more robust analysis (Rovai et al. 2016). For instance, while our model based on the coastal environmental setting framework explains 25% of the litterfall variability in the neotropics, fitting our dataset to latitude (degrees, in module) explains only 11% of the variation in this attribute (adjusted $R^2 = 0.1144$, $df = 69$, F -value = 10.04, P -value = 0.002). In this regard, our model addresses a core question in mangrove macroecology, clarifying what factors control mangrove litterfall at larger spatial scales.

Climatic variables and mangrove productivity

Our results showed that the interaction between P_{\min} and T_{\min} accounted for most of the variability in mangrove litterfall across the neotropics. Temperature and precipitation regimes have long been described as important drivers of mangrove litterfall (Pool et al. 1975, Twilley 1995, Day et al. 1996, Feher et al. 2017). Temperature affects net primary production and growth by influencing rates of photosynthesis and respiration, including reproductive success and C storage (Duke 1990, Lovelock 2008). Similarly, net primary production varies with rainfall (Day et al. 1996, Twilley et al. 1997, Agraz-Hernández et al. 2015), as evidence with lower rates for mangrove forests along dry coastlines, whereas highest litterfall rates were related to areas with rainfall regimes over 2000 mm/yr (Hernández and Mullen 1979, Félix-Pico et al. 2006, Lema and Polanía 2007). The synergism between temperature and precipitation regimes plays a major role in determining mangrove development and distribution (Osland et al. 2016, 2017b, Feher et al. 2017).

Overall, mangroves seem to be greatly influenced by extreme events rather than by average monthly fluctuations (Lovelock et al. 2016). Indeed, one of the longest continuous monitoring of litterfall reported to date, carried out in Términos Lagoon, Mexico, revealed that 74% of the seasonal variability in litterfall was explained by minimum precipitation of dry season, minimum winter temperature, and soil salinity (Day et al. 1996). Thus, the use of extreme values as predictors of mangrove ecosystem functioning can be ecologically more relevant than the use of mean values to account for large-scale temporal

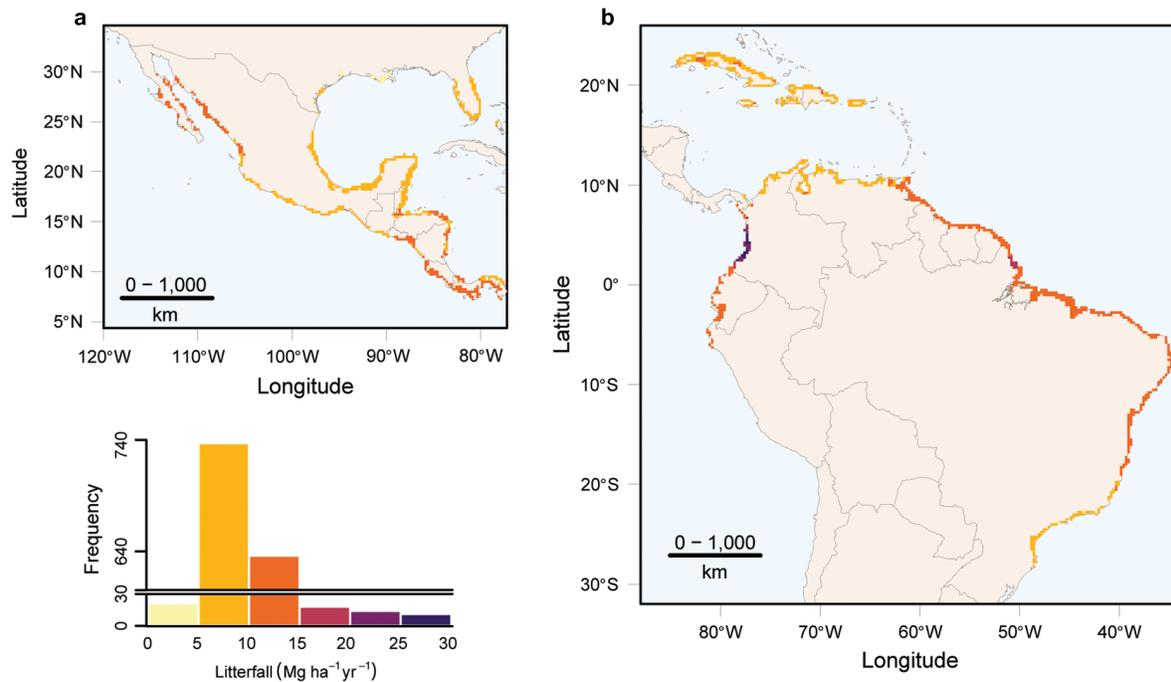


Fig. 3. Mangrove litterfall ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) predicted for the (a) United States, Mexico, and Central America, and (b) South America and Caribbean regions. The histogram depicts the frequency of modeled litterfall rates.

variability in primary productivity (Day et al. 1996, Osland et al. 2013, 2017a, Cavanaugh et al. 2014). Given the ecological importance of those extreme variables to mangrove litterfall, we opted to use precipitation of the driest month and minimum temperature of the coldest month rather than annual means.

Although not selected as a significant term in our model, PET has been acknowledged as one of the major climatic factors determining the distribution of life zones on Earth (Holdridge 1967). Potential evapotranspiration relative to precipitation controls soil moisture, which is the amount of water potentially available to plants serving as an important regulator of forest water balance (Holdridge 1967). The interaction between PET and precipitation is especially important for mangroves, since moisture can influence seasonal soil salinity (Clough 1992, Wolanski et al. 1992, Twilley and Chen 1998). Recent reviews have found that PET is a significant factor explaining global variability of aboveground biomass and soil organic carbon stocks in mangroves (Rovai et al. 2016, 2018). In wet equatorial climates, the ratio of PET to precipitation is lower

where mangrove forests can allocate more energy to their aboveground biomass resulting in taller trees (e.g., height > 20 m; Schaeffer-Novelli et al. 1990, Clough 1992). Where PET exceeds rainfall, decreased soil moisture results in higher soil salinities leading to water stress on mangrove trees and restricted forest development (Schaeffer-Novelli et al. 1990, Day et al. 1996, Twilley and Chen 1998, Castañeda-Moya et al. 2006). Moreover, the upper limit of distribution in the tidal frame and survival of particular mangrove species are mainly determined by soil salinity, which is regulated by the conjunction of PET, rainfall, and tidal amplitude (Wolanski et al. 1992, Castañeda-Moya et al. 2006).

Geophysical variables and spatial patterns of mangrove litterfall

It should be noted that the environmental variables that are represented by terms in the final selected model (Eq. 1) are a product of the automated model selection method used, which was based on AIC. Roughly, the AIC method is based on the trade-off between simplicity (that is, a model with less terms) and goodness of fit. Thus,

interpretation on the ecological significance of any given environmental variable in explaining a functional attribute should not rely solely on AIC, since this method is dependent on the dataset being tested. This is particularly important when considering the spatial representation of both response and environmental variables used as predictors. This spatial heterogeneity issue has been stressed elsewhere and arguably is the cause for the misrepresentation of acknowledged environmental drivers (such as RD and PET, as in this study) in models to estimate mangrove structural and functional attributes at larger scales (Hutchison et al. 2014, 2015, Rovai et al. 2016, 2018).

Our model highlights the role of tides on mangrove litterfall variability at larger spatial scales. These findings support previous studies that show a strong positive influence of tidal amplitudes on net primary production (Cintrón and Schaeffer-Novelli 1981, Alongi 2002). Periodic tidal inundation promotes nutrient exchange and soil aeration, which reduce the accumulation of toxic substances (e.g., sulfides) and enhance forest development (Lugo and Snedaker 1974, Castañeda-Moya et al. 2013). In addition, riverine mangroves are characterized by optimal structural growth, with high values of aboveground biomass and litterfall resulting from high nutrient availability and reduced soil salinity levels, which are controlled by river discharge (Pool et al. 1975, Cintrón et al. 1978, Castañeda-Moya et al. 2006). For instance, the input of allochthonous sediment (i.e., river discharge) increases P concentrations, which lowers the N:P ratio and results in greater forest biomass and productivity (Twilley et al. 2019).

Our model predicted highest litterfall rates in mangrove forests influenced by large river systems, such as in the San Juan River Delta (Colombia), Orinoco Delta (Venezuela), Essequibo River (Guyana), and Amazon Delta (Brazil; Fig. 3). These patterns of high litterfall rates predicted for river-dominated coastlines are consistent with observed values reported for deltaic coastal settings (Fig. 2). These regions are located in tropical regions subjected to low annual variability in temperature, high rates of rainfall (>2000 mm/yr; Hijmans et al. 2005), and macrotidal regimes (Carrère et al. 2012). The highest litterfall rates predicted by our model were in

the Pacific coast of Colombia, reaching $28 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. In addition to high riverine inputs, this region is one of the most humid in the world with annual precipitation exceeding 6000 mm/yr (Hijmans et al. 2005), and tidal amplitudes >4 m at spring tides (Carrère et al. 2012). Consequently, mangroves along the Pacific coast of Colombia are one of the most productive forests in the world exceeding 50 m in height with aboveground biomass values (maximum 413 Mg/ha) among the highest reported for mangroves worldwide (Rovai et al. 2016, Castellanos-Galindo et al. 2017). The values predicted by our model are similar to published litterfall rates of $27.6 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for the Colombian Pacific coast (Hernández and Mullen 1979), and also similar ($20 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) to those reported for a river-dominated coastline in the Colombian Caribbean coast (Lema and Polanía 2007).

Conversely, the lowest litterfall rates were predicted for mangroves in coastal Louisiana, USA, reaching up to $5 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. In contrast to other highly productive deltaic systems, as described above, Louisiana mangroves are located in the northernmost limit of distribution in the neotropics, subjected to frequent frost events (Osland et al. 2013, 2016, 2017a, Cavanaugh et al. 2018). Microtidal regimes and annual precipitation rates of 1600 mm/yr (Henry and Twilley 2013) constrain net primary productivity and forest development in this deltaic region. In regions where mangroves colonize carbonate platforms, such as in Florida, Caribbean Islands, and Yucatan Peninsula, mangrove soils are mostly formed by in situ sedimentation of carbonate (or biogenic formation) and organic production (Woodroffe 1992). Due to the high permeability of this carbonate soil matrix and the lack of riverine input in this setting, P becomes a limiting nutrient for mangrove development (Castañeda-Moya et al. 2011, 2013, Adame et al. 2013, Rovai et al. 2018). Mangrove litterfall in these carbonate platforms is dominated by scrub mangroves with values $<3 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Twilley 1995, Coronado-Molina et al. 2012, Castañeda-Moya et al. 2013; Fig. 3).

The variability in mangrove litterfall rates in carbonate coastlines is comparable to both tide- and wave-dominated estuarine settings (Fig. 2). One explanation is linked to allochthonous nutrient inputs to sites are subjected to hurricane

disturbance. For instance, the high frequency of hurricanes has been correlated with increased long-term deposition of P in mangrove soils across the Florida Coastal Everglades, Yucatan Peninsula, and some Caribbean Islands, contributing to gradients in mangrove forest development (Castañeda-moya et al. 2010, Adame et al. 2013). Gradients of P deposition after the passage of Hurricane Wilma across the Everglades and legacies from previous storms may explain regional patterns of biomass and productivity in this coastal landscape (Chen and Twilley 1999, Castañeda-moya et al. 2010). Thus, disturbance-driven episodic events may explain the high variability in litterfall rates reported for mangrove forest stands developing within carbonate settings (Aké-Castillo et al. 2006, Adame et al. 2013, Danielson et al. 2017). In addition, some P-limited carbonate settings receive nutrient-rich inputs from groundwater sources, allowing for greater forest structural development and increased litterfall rates (Adame et al. 2013, 2017). While our model is limited in accounting for the role of hurricanes and other external nutrient input sources in controlling mangrove litterfall, our model predicts values for Florida ranging from 6 to 9 Mg·ha⁻¹·yr⁻¹ for areas where values between 3 and 10 Mg·ha⁻¹·yr⁻¹ have been reported (Ewe et al. 2006, Castañeda-Moya et al. 2013). However, our model seems to have overestimated litterfall in some regions such as in Baja California, where predicted values range from 10 to 15 Mg·ha⁻¹·yr⁻¹ while reported values average 6 Mg·ha⁻¹·yr⁻¹ (Félix-Pico et al. 2006). Over- or underestimation bias in our model outputs can be attributed to the combination of extreme environmental conditions (for instance, aridity along Gulf of California) and lack of data that adequately represent the response variable under drier climate conditions.

At local scales, geomorphology, species interaction, availability of critical resources (light, nutrients, space), regulators (pH, salinity, sulfide), and hydroperiod are major drivers of mangrove functional and structural traits (Woodroffe 1992, Castañeda-Moya et al. 2013, Twilley et al. 2019). Depending on the magnitude of such interactions, litterfall rates as well as biomass allocation and growth rates may be distinct among mangrove ecotypes (for instance, riverine

vs. scrub sites) within the same type of coastal environmental setting and same latitude (Castañeda-Moya et al. 2013, Twilley et al. 2019). Therefore, we believe that uncertainty in litterfall associated with spatial variability generated by our model is likely due to local environmental drivers regulated by hydroperiod. Unfortunately, there are no environmental gridded data available that adequately constrain hydroperiod within hydrogeomorphic zones that allow for modeling such variability in litterfall at continental or global scales. Our results highlight underrepresented coastlines in terms of data availability, particularly near the limits of mangrove distribution. For instance, while some mangrove stands are well studied, with numerous sampling points and continuously evaluated throughout many years, some areas completely lack litterfall data (for instance, central and northern coasts of Brazil, Louisiana and Texas coasts, west coasts of Mexico and Central America, as well as Cuba and almost all the Caribbean Islands). These data gaps highlight the need for further studies, especially near or at mangrove range limits, where limiting environmental conditions such as freezing events, aridity, and extreme seasonality prevail.

Global implications for carbon budgets

Our model is a useful tool to capture potential changes in mangrove litterfall under different climate change scenarios. In regions expected to observe an increase in aridity coupled with increase in temperature patterns such as in the Caribbean Islands (IPCC 2013, Ward et al. 2016), the combined effect of reduced input of freshwater and increased potential evaporation could significantly increase soil salinity and sulfide concentrations, and thus decrease litterfall (Field 1995, Snedaker 1995). Conversely, in areas where an increase in rainfall is expected, higher freshwater and nutrient input could lower the effect of anoxic conditions and enhance mangrove litterfall (Field 1995, Gilman et al. 2008, Osland et al. 2017b). Changes in precipitation patterns will likely have a major effect in areas with limited rainfall. Drier conditions will likely lead to replenishment of mangroves for salt flats, while wetter conditions should enhance mangrove expansion (Osland et al. 2017b). Although increases in precipitation have been positively

correlated with litterfall, greater freshwater input to mangroves adjacent to large river systems (i.e., Amazon and Parnaíba estuaries in Brazil) could lead to replacement of mangroves by riparian vegetation (França et al. 2012). Similarly, changes in tidal regimes coupled with projected sea-level rise will likely play a major influence in total mangrove net primary productivity patterns, and mangroves located in microtidal regimes will be at greatest risk, due to their lower elevation capital (Lovelock et al. 2015). While predicted responses of mangroves to distinct climate scenarios may carry a large degree of uncertainty, our results can be used as a reference layer for modeling approaches that focus on changes in ecosystem's traits in response to future climate conditions. This is particularly relevant to range limits where changes in vegetation greening and browning patterns revealed by Enhanced Vegetation Index, and thus productivity, clearly respond to long-term climate oscillations (Cavanaugh et al. 2018).

To date, most studies focus on C stocks, mainly in the soil (Jardine and Siikamäki 2014, Atwood et al. 2017, Rovai et al. 2018, Twilley et al. 2018). Unquestionably, C stocks are an important attribute of blue carbon ecosystems (mangroves, salt marshes, seagrass meadows) considering that the degradation of these ecosystems can lead to massive release of CO₂ into the atmosphere. However, significant CO₂ emissions may only result if soil carbon is exposed (i.e., excavation for shrimp ponds) or mangrove wood is burned (i.e., mangrove wood used for charcoal). While these activities, among others, are major threats to mangrove ecosystems in certain nations, CO₂ emissions from mangrove deforestation alone do not account for the capacity of such ecosystems to mitigate current CO₂ emission rates. Instead, C flux rates may be more representative of the capacity of mangroves to offset current CO₂ emission rates, allowing for improvement of the coastal blue C budget. Indeed, C fixed through litterfall is a major process for C balance between mangroves and adjacent coastal waters considering that 50% of litterfall is exported to estuaries and coastal oceans (Jennerjahn and Ittekkot 2002). Based on these proportions we estimate that out of total annual mangrove litterfall in the neotropics, 5.8 TgC/yr are exported to adjacent waters. This estimate of C export for the

neotropics corresponds to nearly 30% of the global C exported by tides annually (that is, 20 TgC/yr; based on Bouillon et al. 2008; using mangrove surface area coverage by Hamilton and Casey (2016), and carbon conversion factor by Hamilton and Friess 2018). Moreover, we estimated an average litterfall of 10.25 Mg·ha⁻¹·yr⁻¹ (that is, 512 gC·m⁻²·yr⁻¹) for the neotropics. At 50% export rate, this per-area basis estimate is very similar to mean global values reported earlier (C export rate of 210 gC·m⁻²·yr⁻¹; Twilley et al. 2017).

Global estimates of C fluxes in mangroves are generally based on mean reference values calculated from published data, which are then extrapolated to a per-area basis (Twilley et al. 1992, Bouillon et al. 2008). Our updated estimate of mangrove litterfall in the neotropics (that is, 5 MgC·ha⁻¹·yr⁻¹) shows that this process has been underestimated between 20% and 50% relative to mean reference values available in the literature (e.g., 4.12 MgC·ha⁻¹·yr⁻¹, Bouillon et al. 2008; 3 MgC·ha⁻¹·yr⁻¹, Twilley et al. 2017). Coupling our estimates of C fixed in litterfall for the neotropics with a global mangrove surface coverage area of 81,848.87 km² (Hamilton and Casey 2016), we estimate global mangrove C fixed in litterfall at 42 TgC/yr. This global estimate is 5% higher than predicted earlier (Bouillon et al. 2008). Although previous estimates based on mean reference values may not differ substantially from ours, they do not capture the spatial variability of mangrove litterfall. To our knowledge, our study is the first to quantify and map the spatial variability of C fixed in litterfall in mangrove forests at continental scale in response to geophysical and climatic environmental drivers. Our results strengthen the global C budget for coastal wetlands, providing blue carbon scientists and coastal policy makers with a more accurate representation of the potential of mangroves to offset CO₂ emissions.

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