Universidade Federal de Santa Catarina

Programa de Pós-Graduação em Ecologia

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Campus Universitário Trindade

Florianópolis- SC

Dissertação apresentada ao Programa de Pós-graduação em Ecologia, Departamento de Ecologia e Zoologia, do Centro de Ciências Biológicas da Universidade Federal de Santa Catarina, como requisito para obtenção do Título de Doutor em Ecologia

Orientador: Paulo Roberto Pagliosa Alves

Coorientador: Robert R. Twilley

Assinatura energética e estoque de carbono na biomassa aérea e em solos de manguezais na região Neotropical

André Scarlate Rovai

Florianópolis, 2016

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ASSINATURA ENERGÉTICA E ESTOQUE DE CARBONO NA BIOMASSA AÉREA E EM SOLOS DE MANGUEZAIS NA REGIÃO NEOTROPICAL

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutor em Ecologia
Orientador: Prof. Dr. Paulo Roberto Pagliosa Alves
Coorientador: Prof. Dr. Robert R. Twilley

Florianópolis
2016

"Assinatura energética e estoque de carbono na biomassa aérea e em solos de manguezais na região Neotropical"

Por

André Scarlate Rovai

Tese julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (08/PPGECO/2016) do Programa de Pós-Graduação em Ecologia - UFSC.
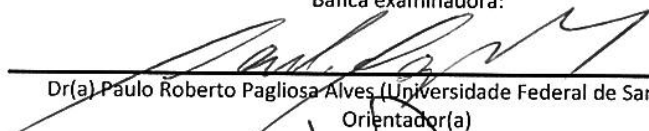
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Prof(a). Dr(a). Nivaldo Peroni
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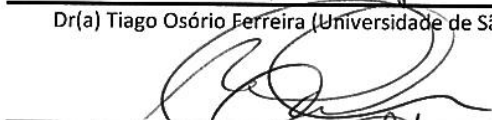
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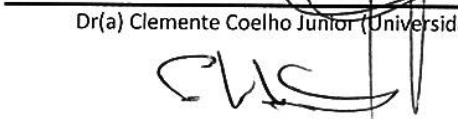
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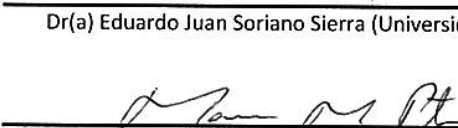
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Florianópolis, 08 de Junho de 2016.

I dedicate this work to my boys, Enzo e Lino. May your dreams never fade. I love you.

AGRADECIMENTOS

This is science that cannot be done behind a desk or by a committee.

(Thor Heyerdahl, 1947)

RESUMO

O presente trabalho teve por objetivo investigar os padrões latitudinais dos estoques de carbono (C) na biomassa aérea, bem como a concentração e razão estequiométrica dos elementos C, nitrogênio (N) e fósforo (P) em solos de manguezais da região Neotropical. Em relação ao estoque de C na biomassa aérea, foi hipotetizado que a variabilidade espacial da biomassa aérea em manguezais é controlada tanto por fatores climáticos, quanto geofísicos. Primeiramente, foi desenvolvido um modelo alométrico que estima valores de biomassa aérea (t ha^{-1}) em nível de sítio a partir de dados de inventários florestais (i.e., área basal e altura médias). Este modelo foi validado (análise por modelo nulo) e se mostrou adequado, apresentando valores semelhantes aos observados (p=0,34). Um segundo modelo preditivo (regressão múltipla), baseado em dados de 1047 sítios, provenientes de 134 estudos independentes (publicados e inéditos), foi então elaborado com a finalidade de estimar a biomassa aérea de manguezais em escala hemisférica. Os resultados mostraram que cerca de 20% da variabilidade espacial da biomassa aérea de manguezais é explicada por maiores amplitudes de marés, elevadas temperaturas e pluviosidade e reduzida evapotranspiração, resultando em valores mínimos e máximos de 16,6 e 627,0 t ha^{-1}, respectivamente (média de 88,7 t ha^{-1}), para a área de estudo. Os resultados do presente estudo evidenciam que a biomassa aérea de manguezais na área de estudo tem sido superestimada entre 25 e 50%. Em relação ao compartimento edáfico, foi hipotetizado que variabilidade latitudinal da concentração de C, N e P, bem como da razão estequiométrica destes elementos em solos de manguezais, é explicada pela eco-geomorfologia costeira (i.e., fatores regionais) em contraposição a fatores de macro-escala (i.e., gradiente latitudinal). Para testar esta hipótese foram coletadas amostras de solo de manguezais em 27 locais distribuídos na região Neotropical, entre as latitudes ~29,5°N e 27,5°S, representando diferentes ambientes geomorfológicos costeiros. A variabilidade espacial na concentração de P (g cm^{-3}) não foi explicada pela latitude (R^2=-0,01, p=0,52, df=79). Em contrapartida, foram observados aumentos nas concentrações de C orgânico e N total com a latitude (R^2=0,19 e 0,27, respectivamente; α<0,05 para esta e analises seguintes). As razões N:P e C:P também aumentaram com a latitude (R^2=0,19 e 0,10), enquanto que a razão C:N diminui (R^2=0,05). Os componentes de variação (CV) da ANOVA bi-fatorial (fatores ambiente geomorfológico costeiro e sítio) revelaram que a variabilidade

latitudinal na concentração e razão estequiométrica destes elementos está relacionada aos tipos de ambientes geomorfológicos costeiros (42% para P a 64% para N), enquanto que o fator sítio explicou apenas uma pequena proporção da variabilidade (16% para N e 40% para P). A existência de grupos representando ambientes costeiros distintos foi constatada por análises multivariadas (nMDS, PERMANOVA). Além dos agrupamentos, tais análises também revelaram a formação de um gradiente ordenado desde sítios com limitação de nutrientes (alta razão N:P), e que recebem pouco ou nenhum aporte de água doce (descarga de rios), até sítios que recebem contribuições significativas de águas continentais e apresentam baixas razões N:P no solo. É proposto um arcabouço objetivando fomentar a concepção de modelos preditivos mais robustos, alinhados assim com agendas internacionais como aquelas estabelecidas pelo IPCC, UNFCCC e programas REDD+.

Palavras-chave: Biomassa aérea. Macroecologia. Neotropico. Manguezal. Assinatura energética. Carbono do solo. Nitrogênio do solo. Fósforo do solo. Estequiometria.

ABSTRACT

This study's goal was to assess the latitudinal patterns o carbon (C) storage in mangrove aboveground biomass (AGB) as well as the concentration and stoichiometry of C, nitrogen (N) and phosphorus (P) in mangrove soils across the Neotropics. With regards to C storage in mangrove AGB it was hypothesized that the combination of climatic and geophysical environmental forcings drive the latitudinal variation in mangrove AGB. First, an allometric model that predicts AGB values (t ha^{-1}) at the site level using existing forest structure inventories (e.g., mean basal área and height) was developed. This model was validated (null models analysis) and proved efficient in predicting mangrove AGB estimates similar to observed values (p=0,34). Second, a predictive model (multiple regression) using data from 1047 sites, compiled form 134 independent studies (published and unpublished), was developed to predict mangrove AGB at hemispheric scales. Our findings showed that about 20% of the spatial variability in mangrove AGB was explained by higher tidal amplitudes, river discharge, temperature, direct rainfall and decreased potential evapotranspiration. The model's outputs for the study area ranged from 16.6 to 627.0 t ha^{-1} (mean, 88.7 t ha^{-1}). Our findings show that mangrove AGB has been overestimated by 25–50% in the Neotropics. Regarding the edaphic compartment, it was hypothesized that the latitudinal variation in mangrove soil C, N, and P concentration and stoichiometry is explained by the coastal ecogeomorphology (e.g., regional factors) rather than the latitudinal gradient. To test our assumptions we sampled soil cores from 27 sites across the Neotropics, spanning from ~29.5°N e 27.5°S, and representing a variety of coastal environmental settings. P concentration (g cm^{-3}) was not correlated with latitude (OLS; R^2=-0.01, p=0.52, df=79). Contrary, C and N increased with latitude (R^2=0.19 and 0.27, respectively; α<0.05 for this and following analyses). The molar ratios N:P and C:P also increased with latitude (R^2=0.19 and 0.10), while the C:N ratio decreased with it (R^2=0.05). The components of variation (CV) of the two-way ANOVA (factors: coastal environmental setting and site) indicated the coastal environmental settings explained most of the variation in mangrove soil properties (ranging from 42% for P to 64% for N), with sites accounting for a smaller portion of the variability (16% for N, and 40% for P). The cohesion of groups representing distinct coastal environmental settings was tested using multivariate analyses (nMDS, PERMANOVA). These analyses evidenced the

formation of groups and a gradient spanning from nutrient-limited sites (higher soil N:P ratios), with little or no freshwater input (river discharge), to sites that receive significant river input and have low soil N:P ratios. A framework to improve the development of more robust predictive models is proposed, meeting highest accuracy standards established by international agends such as the IPCC, UNFCCC e REDD+ programmes.

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LISTA DE QUADROS

LISTA DE ABREVIATURAS E SIGLAS

AGB – Aboveground biomass (biomassa aérea)
AIC – Akaike's information criterion (critério de informação de Akaike)
BA – Basal área (área basal)
C – Carbon (carbono)
C:N:P – Razão estequiométrica Carbono:Nitrogênio:Fósforo
CES – Coastal environmental setting (ambiente geomorfológico costeiro)
CO_2 – Carbon dioxide (dióxido de carbono)
D – Density (densidade)
d.b.h. – Diameter at breast height (diâmetro a altura do peito)
ESH – Environmental signature hypothesis (hipótese da assinatura energética
F – Form fator (fator de forma)
GDD – Growing degree-days
H – Height (altura)
IPCC – Intergovernmental Panel on Climate Change
k – constant 0.0000785 for QSD in cm (constante 0.0000785 para QSD em cm)
N – Nitrogen (nitrogênio)
NPP – Net primary productivity (produção primária líquida)
OLS – Ordinary least squares (mínimos quadrados ordinários)
P – Phosphorus (fósforo)
PET – Potential evapotranspiration, in mm year^{-1} (evapotranspiração potencial, em mm year^{-1})
Pmin – Precipitation of the driest month, in mm year^{-1} (precipitação do mês mais seco, em mm year^{-1})
QSD – Quadratic mean diameter (diâmetro médio quadrático)
RD – River discharge, in m^3 s^{-1} (descarga fluvial, em in m^3 s^{-1})
REDD+ – Program on reducing emissions from deforestation and forest degradation
Tmin – Minimum temperature of the coldest month, in °C (temperatura mínima do mês mais frio, em °C)
TR – Tidal range, in cm (amplitude de marés, em cm)
UNFCCC – United Nations Framework Convention on Climate Change
VIF – Variance inflation fator (fator de inflação da variância)
WSG – Wood specific gravity (gravidade específica da madeira)

SUMÁRIO

1 INTRODUÇÃO

Manguezais são ecossistemas estuarinos tropicais e subtropicais geralmente dominados por formações florestais típicas, de porte variável (de arbustivo a árvores com até ~50 metros de altura), e adaptadas morfo e fisiologicamente a gradientes ambientais condicionados pela alternância de períodos submersos (inundação pelas preamares) e de exposição aérea. Embora usualmente colonizados por plantas vasculares (angiospermas), estes sistemas apresentam elevada resiliência, podendo, em resposta a variações climáticas (p. ex., evapotranspiração superior a precipitação) e geofísicas (oscilações no nível médio relativo do mar, alterações no aporte sub e superficial de águas continentais), manifestar feições conspícuas (*alternate states*; sensu HOLLING, 1973) como, por exemplo, planícies hipersalinas desprovidas de vegetação vascular, denominadas popularmente como "apicuns" ou "salgados" (ROVAI *et al.*, 2012; SCHAEFFER-NOVELLI *et al.*, 2016).

Figura 6 - Distribuição global de manguezais. A escala de cores indica a diversidade de espécies vegetais típicas de mangue. Extraído de POLIDORO *et al.* (2010).
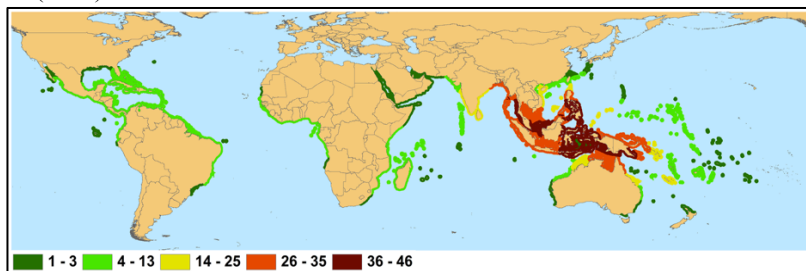
Ainda que em determinadas paisagens do globo fatores locais e regionais sejam preponderantes para os limites latitudinais de manguezais (Figura **6**), em geral tanto a amplitude de distribuição hemisférica quanto o desenvolvimento estrutural de manguezais são determinados pelas temperaturas mínimas do ar dos meses mais frios (CHAPMAN, 1975; LUGO; ZUCCA, 1977; OSLAND *et al.*, 2016; ROVAI, *et al.*, 2016). Entretanto, ao longo desse continuum climático, manguezais se desenvolvem em uma diversidade de ambientes costeiros (Figura **7**), caracterizados por diferentes energias subsidiarias, cujas intensidades variam em função da geomorfologia costeira (THOM, 1982; WOODROFFE, 1992).

Figura 7 - Ambientes geomorfológicos costeiros onde os manguezais predominantemente se desenvolvem. a-planície deltaica, b-estuário, c-laguna, d-plataforma carbonática. Extraído de WOODROFFE *et al.* (2016).
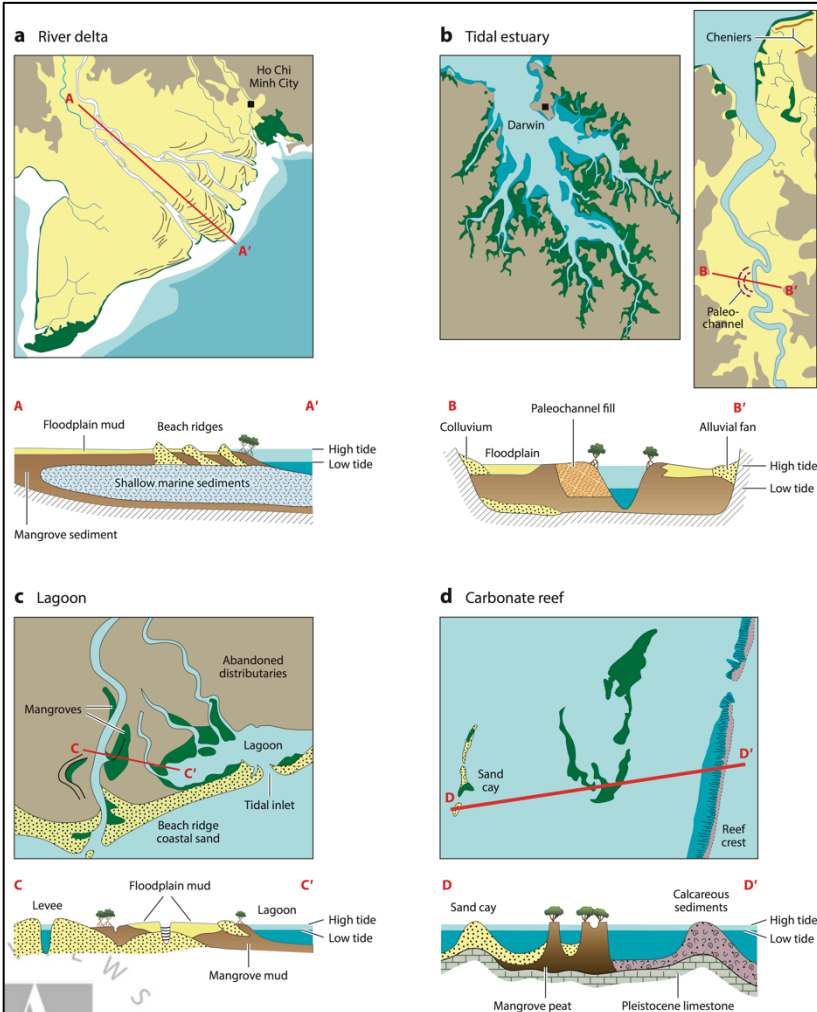
Coletivamente, mecanismos regulados pela interação entre geomorfologia costeira e fatores geofísicos (energia das ondas, amplitude de marés, descarga de águas continentais), climáticos

(temperatura, precipitação e evapotranspiração) e biológicos (taxas metabólicas), conferem a ambientes costeiros uma assinatura energética peculiar, atuando desde a seleção do tamanho dos grãos até os teores de matéria orgânica, aporte de nutrientes essenciais (p. ex., fósforo em deltas vs. sistemas carbonáticos), teor de água intersticial, taxas de decomposição e estruturação da camada redox, resultando, portanto, na enorme variabilidade estrutural e funcional de manguezais observada em qualquer latitude (TWILLEY; RIVERA-MONROY, 2009; TWILLEY; CHEN; HARGIS, 1992; TWILLEY, 1995). Em virtude de sua elevada diversidade estrutural e funcional, manguezais são caracterizados por ampla plasticidade em termos de provisão de serviços ecossistêmicos à humanidade (EWEL; TWILLEY; ONG, 1998).

Avaliações ecológico-econômicas revelam que manguezais estão entre os sistemas naturais mais valiosos do planeta, considerando serviços ambientais como produtividade primária e manutenção da biodiversidade e de estoques pesqueiros, estabilidade e proteção da linha de costa contra eventos extremos, controle da poluição e balanço climático (COSTANZA et al., 2014). No entanto, a despeito do seu relevante impacto positivo para o ambiente e sociedade, estes sistemas vem desaparecendo a taxas alarmantes em virtude de ocupações irregulares na zona costeira, represamento e desvios de cursos d'água a montante das bacias hidrográficas, expansão de atividades portuárias e carcinicultura (DUKE et al., 2007; PAGLIOSA; ROVAI; FONSECA, 2012). Estima-se que para compensar taxas atuais de perdas globais, seria necessário recuperar 150.000 hectares de manguezais por ano (LEWIS, 2011). Embora pareça haver consenso científico sobre métodos eficazes para a restauração destes sistemas, a maioria dos projetos de recuperação de manguezais, independente da escala (local-global), fracassam em virtude da inobservância de conceitos ecológicos básicos (DALE; KNIGHT; DWYER, 2014; LEWIS, 2005).

Particularmente, o papel destes ecossistemas na ciclagem do carbono atmosférico (CO_2) e na mitigação do efeito estufa são notadamente reconhecidos (DONATO et al., 2011; TWILLEY; CHEN; HARGIS, 1992). O mecanismo usado por manguezais para estocar e preservar o carbono (C) é semelhante ao de ecossistemas terrestres: fixa CO_2 e o incorpora nas biomassas aérea (troncos, galhos e folhas) e subterrânea (raízes). Contudo, os principais aspectos que diferenciam o acúmulo e o estoque do C nos solos de manguezais são as elevadas taxas de acréscimo e o tempo de residência deste elemento na coluna sedimentar, que pode atingir milênios devido a combinação entre elevadas taxas de sedimentação e baixa oxidação da matéria orgânica

(raízes mortas, serapilheira, C de origem aloctone) em virtude da condição saturada do solo mantida por pulsos diários de inundação (DUARTE; MIDDELBURG; CARACO, 2005). Como nestes ambientes o nível topográfico do solo tende a acompanhar a elevação do nível do mar, o estoque do C no solo aumenta juntamente com o incremento do volume de sedimento ao longo do tempo (CHMURA *et al.*, 2003). A conservação deste C, referido recentemente como "carbono azul", possui importância estratégica para políticas voltadas para a captação dos gases de efeito estufa e mitigação do aquecimento global (COPERTINO, 2011). A destruição e degradação de manguezais convertem esses sumidouros naturais em emissores de CO_2 para a atmosfera, agravando ainda mais o efeito estufa. Em ecossistemas impactados ou destruídos, o C sequestrado ao longo de centenas ou milhares de anos e depositado em espessas camadas do solo e na vegetação é liberado em curto prazo (Figura **8**).

Figura 8 - Principais reservatórios e rotas do carbono atmosférico em manguezais. Extraído de BOUILLON *et al.* (2008).
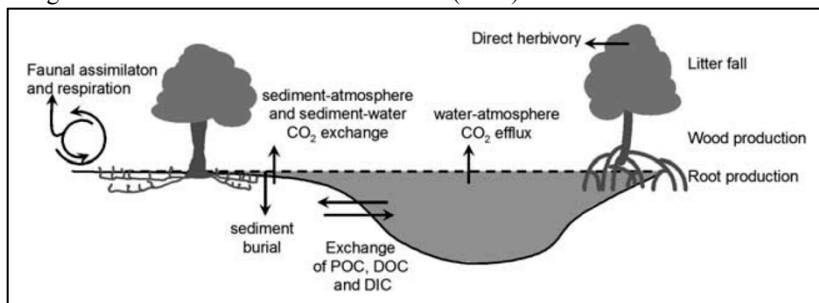
A magnitude destas emissões tornou-se evidente apenas recentemente e tais fontes ainda não têm sido consideradas nas contabilidades nacionais das emissões e nas regulamentações e políticas existentes sobre mudanças climáticas (COPERTINO, 2011). Consequentemente, esta temática tem dominado o cenário recente de investigações científicas com o foco voltado para modelos preditivos capazes de prover estimativas dos estoques de carbono presentes na biomassa aérea e subterrânea de manguezais (HUTCHISON *et al.*, 2014; JARDINE; SIIKAMÄKI, 2014; ROVAI *et al.*, 2016). Em geral, estes estudos convergem em reconhecer as limitações destes modelos em fornecer representações adequadas da variabilidade espaço-temporal no estoques de carbono em manguezais, em parte devido a escassez de

dados bióticos (variável resposta) e adequabilidade de dados abióticos (variáveis explicativas) usados para calibrar os modelos, mas também por negligenciarem fatores locais e regionais que contribuem para padrões observados em escalas maiores (ROVAI *et al.*, 2016).

O objetivo geral do presente trabalho foi investigar os fatores ambientais reponsáveis pela variabilidade latitudinal da biomassa aérea e dos estoques e razão estequiométrica de carbono (C), nitrogênio (N) e fósforo (P) em solos de manguezais na região Neotropical. Os objetivos específicos foram:

- Realizar levantamento sitemático de informações sobre biomassa aérea e características estruturais de manguezais em escala global, com ênfase na região Netropical;
- Validar para manguezais um modelo universal que estima biomassa aérea em nível local (*site*) a partir de inventários florestais existentes (área basal e altura médias);
- Desenvolver modelo preditivo baseado em variáveis climáticas e geofísicas para estimar a biomassa aérea de manguezais em escalas continentais;
- Comparar os resultados do modelo desenvolvido para estimar a biomassa aérea de manguezais com modelos propostos anteriormente;
- Estimar os estoques e razões estequiométricas de C, N e P em solos de manguezais da região Netropical;
- Determinar quantitativamente a influência de forçantes climáticas e geofísicas na formação de ambientes geomorfológicos costeiros conspícuos; e
- Avaliar a influência da variação latitudinal absoluta e de ambientes geomorfológicos costeiros distintos nos estoques e razões estequiométricas de C, N e P em solos de manguezais da região Netropical

1.1 VARIABILIDADE LATITUDINAL DOS ESTOQUES DE CARBONO NA BIOMASSA AÉREA DE MANGUEZAIS

A biomassa aérea representa uma porção significativa do estoque total (vegetação e solos) de carbono orgânico em manguezais (LUGO; SNEDAKER, 1974). Estimativas tradicionais de biomassa aérea incluem o crescimento das árvores e a produção de serapilheira, os quais também contribuem para gênese do solo ao longo do tempo (RIVERA-MONROY *et al.*, 2013; TWILLEY; CHEN; HARGIS, 1992). Ainda, a

variação espaço-temporal dos estoques de carbono na biomassa responde a combinação entre o regime climático, geomorfologia costeira e variáveis geofísicas (TWILLEY; RIVERA-MONROY *et al.*, 2009). Em geral, a produtividade primária líquida e o acúmulo de biomassa em manguezais são maiores em regiões costeiras onde a vazão de rios, amplitude de marés e precipitação são mais abundantes, em contraposição a ambientes marginais (p. ex., baixas temperatura e precipitação, secas periódicas, hipersalinidade), onde a biomassa aérea é significativamente menor (SCHAEFFER-NOVELLI *et al.*, 1990; TWILLEY, 1995). No entanto, a relação entre a interação destas variáveis e a produtividade em manguezais (acúmulo de biomassa, serapilheira) ainda nao foi sistematicamente testada. Consequentemente, predições acerca dos estoques de carbono na biomassa aérea de manguezais são baseadas na premissa de que a variabilidade espacial destas reservas é inteiramente explicada pelo gradiente latitudinal (SAENGER; SNEDAKER, 1993; TWILLEY; CHEN; HARGIS, 1992).

Figura 9 - Classificação hierárquica utilizada para descrever as características estruturais e funcionais de manguezais considerando fatores globais, geomorfológicos (regionais) e ecológicos (locais) que controlam a concentração de nutrientes e o gradiente físico-químico do solo. Extraído de TWILLEY; RIVERA-MONROY (2009).
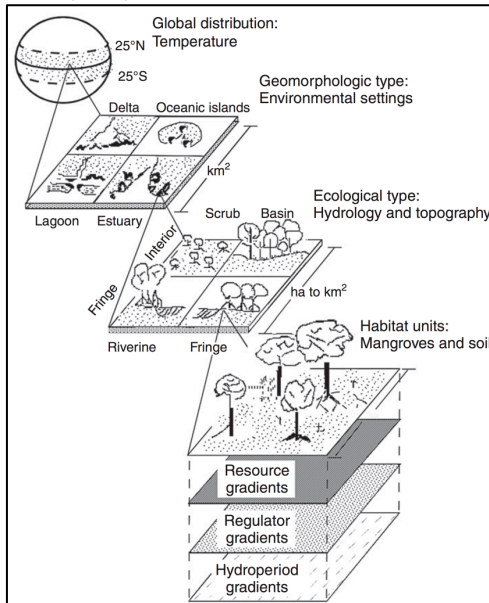
Estimativas globais de biomassa aérea em manguezais são limitadas pela validade e precisão de modelos com diferentes resoluções espaciais como, por exemplo, a generalização de equações alométricas específicas para diferentes comunidades ou ambientes costeiros tropicais e subtropicais diversificados. O desenvolvimento destes modelos depende primariamente de uma boa representatividade (suficiência amostral), o que, por sua vez, demanda extensiva coleta e processamento de dados, quase sempre limitados por recursos financeiros, logísticos e humanos. Estes fatores são responsáveis pela reduzida disponibilidade e desigual distribuição de dados, limitando a precisão de estimativas globais de biomassa aérea em manguezais (SIFLEET; PENDLETON; MURRAY, 2011). Consequentemente, estimativas recentes foram comprometidas devido a escassez de dados na escala de sítio, além da inobservância de variáveis ambientais significativas para variabilidade latitudinal da biomassa aérea de manguezais (HUTCHISON *et al.*, 2014). Ainda, outras abordagens simplesmente consideram valores médios de biomassa aérea de manguezais por faixa ou zona latitudinal e os extrapolam para escala global (SAENGER; SNEDAKER, 1993; TWILLEY; CHEN; HARGIS, 1992). Combinações de modelos para estimar a biomassa aérea de manguezais em escala continental, a partir de informações disponíveis em nível local, ainda não foram sitematicamente testadas.

No capítulo 2 (*Scaling mangrove aboveground biomass from site-level to continental-scale*) deste trabalho foram desenvolvidos modelos estatísticos que estimam a biomassa aérea de manguezais em escalas continentais a partir de dados estruturais de bosques de mangue em nível local, utilizando-se a região Neotropical como área de estudo. Estes modelos foram desenvolvidos com base em dados publicados e não publicados sobre estrutura de bosques de mangue nas Américas, onde cerca de 26% da área global total de manguezais estão localizados. Primeiramente, foi desenvolvido um modelo que estima a biomassa aérea de manguezais em nível local (p. ex., comunidade), utilizando-se para isso dados existentes de estrutura florestal de bosques de mangue (p. ex., área basal e altura médias). Esta etapa possibilitou uma representatividade muito maior da variável-resposta (biomassa aérea) ao longo da área de estudo e, consequentemente, o desenvolvimento de um segundo e mais robusto modelo preditivo, que estima a biomassa aérea de manguezais em escalas continentais. As premissas observadas basearam-se na hipótese da assinatura energética de ambientes costeiros, a qual postula que forçantes geofísicas, conjuntamente com arranjos climáticos regionais, determinam a estrutura (p. ex., área basal, altura) e

o funcionamento (produtividade primária) de ecossistemas costeiros tropicais (TWILLEY, 1995). A hipótese do presente trabalho foi que maiores amplitudes de marés, descarga de rios, precipitação e menor evapotranspiração propiciam maior acúmulo de biomassa aérea em manguezais. Por fim, a performance dos modelos gerados foi avaliada contrastando-se os resultados obtidos com modelos pretéritos baseados na variação latitudinal absoluta (SAENGER; SNEDAKER, 1993; TWILLEY; CHEN; HARGIS, 1992) e em variáveis puramente climáticas (HUTCHISON *et al.*, 2014). Os resultados do presente trabalho geram ferramentas mais precisas para estimar os estoques de C na biomassa aérea de manguezais, otimizando estimativas globais por meio da re-utilização de dados tanto em escala local (sítio) quanto continental.

1.2 VARIABILIDADE LATITUDINAL DE CARBONO, NITROGÊNIO E FÓSFORO EM SOLOS DE MANGUEZAIS

Zonas úmidas costeiras sequestram carbono atomsférico (CO_2) e o armazenam em seus solos onde fica estável por milênios (BOUILLON, 2011). Ademais, estes ecossistemas funcionam como uma "bomba" de carbono (C), convertendo CO_2 em matéria orgânica e exportando-a para os assoalhos marinho-costeiros (BAUER *et al.*, 2013). Em especial, manguezais desempenham um papel fundamental na ciclagem do C atmosférico (TWILLEY; CHEN; HARGIS, 1992), armazenando em média 5 vezes mais C em seus solos do que outros ecossistemas tropicais, temperados e boreais, por unidade de área (ALONGI, 2014; DONATO *et al.*, 2011) (Figura **10**). Considerando que a interação entre C, nitrogênio (N) e fósforo (P) pode aumentar ou enfraquecer o balanço climático (ALLISON; WALLENSTEIN; BRADFORD, 2010; JANSSENS *et al.*, 2010), a conjugação de mecanismos de micro e macro escala reponsaveis pela assinatura energética (p. ex., carbono:nitrogênio:fósforo ou razão estequiométrica C:N:P) em manguezais é fundamental para o avanço do conhecimento e melhoria de modelos preditivos que almejam explicar a variação latitudinal relacionada a disponibilidade de nutrientes e aos estoques de C nestes ecossistemas, bem como em outras zonas úmidas costeiras.

Embora não seja objetivo do presente capítulo engendrar uma revisão sitemática sobre macroecologia de manguezais e hipóteses correlatas, notadamente esta ciência permanece como emergente, com apenas poucos estudos dedicando-se a elucidar questões ecológicas em

escalas maiores de observação (ELLISON, 2002; LOVELOCK *et al.*, 2007). Em contrapartida, a ampla distribuição geográfica ao longo dos litorais tropicais e subtropicais do planeta (GIRI *et al.*, 2011), ocupando uma grande diversidade de ambientes geomorfológicos costeiros (deltaico, carbonático, estuarino), características evolutivas bem definidas e a baixa complexidade de habitats, fazem dos manguezais um exelente ecossistema para aplicação em investigações macroecológicas (ELLISON, 2002).

Figura 10 - Comparação dos estoques de C em manguezais e outros ecosistemas tropicais, tempreados e boreais. Extraído de DONATO *et al.* (2011).
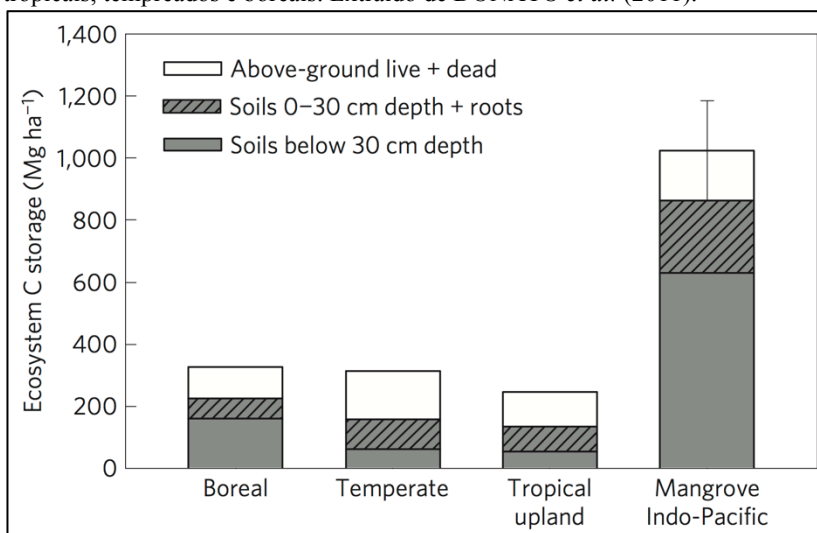
Os padrões de macroecológicos de conservação de nutrientes e estratégias de alocação de C descritos para manguezais foram alicerçados em teorias desenvolvidas para florestas de terras emersas. Por exemplo, a Hipótese Geoquímica, a qual afirma que solos de florestas emersas tropicais são mais intemperizados, portanto têm menor disponibilidade de P, foi proposta para explicar a variação latitudinal da limitação de P em solos de manguezais (LOVELOCK *et al.*, 2007), o que por sua vez é intrinsicamente relacionado as estratégias de partição de C da vegetação (CASTAÑEDA-MOYA; TWILLEY; RIVERA-MONROY, 2013). Adicionalmente, a escassez e distribuição desigual de dados associada a seleção arbitrária de variáveis ambientais utilizadas em modelos contemporâneos que estimam a concentração de C em solos

de manguezais (JARDINE; SIIKAMÄKI, 2014), têm retardado o desenvolvimento de modelos preditivos capazes de estimar com maior precisão os estoque de C em níveis regional e global. Outras abordagens incluem a aparente relação alométrica entre biomassa aérea e subterrânea (HUTCHISON *et al.*, 2014). Enquanto estes modelos proporcionam um primeiro olhar sobre a distribuição e magnitude dos estoques de C em solos de manguezais, eles desconsideram teorias relativas a conservação de nutrientes (CHAPIN III; VITOUSEK; VAN CLEVE, 1986; VITOUSEK; FARRINGTON, 1997) e a ecogeomorfologia (THOM; WRIGHT; COLEMAN, 1975; THOM, 1967, 1982; WOODROFFE, 1992), além de simplificarem o conjunto de variáveis ambientais relevantes para a estequiometria em solos de manguezais e sua influência nas estratégias ecossistêmicas de alocação de C.

O capitulo 3 (*Ecogeomorphology drives latitudinal variation in coastal wetlands soil properties*) deste trabalho avaliou a variabilidade latitudinal relativa a limitação de nutrientes (N e P) e estoque de C em solos de manguezais. Foram determinadas a concentração e a estequiometria de C, N e P em solos de manguezais coletados em 27 locais, incluindo diferentes tipos de ambientes geomorfológicos costeiros, os quais foram replicados ao longo da região Neotropical (desde ~ 29.5°N até 27.5°S). Foi hipotetizado que a ecogeomorfologia, e não o gradiente latitudinal, determina a variabilidade em macro escala na assinatura energética em solos de manguezais e discute implicações para estimativas recentes de estoque de C nestes ecossistemas. Foi hipotetizado também que fatores regionais, incluindo forçantes geofísicas (descarga de rios), consorciadas ao clima (temperatura, precipitação e evapotranspiração), formam distintos ambientes geomorfológicos costeiros, os quais determinam a disponibilidade de nutrientes e a magnitude dos estoques de C nos solos de manguezais.

2 SCALING MANGROVE ABOVEGROUND BIOMASS FROM SITE-LEVEL TO CONTINENTAL-SCALE[1]

2.1 ABSTRACT

Aim. We developed a set of statistical models to improve spatial estimates of mangrove aboveground biomass (AGB) based on the environmental signature hypothesis (ESH). We hypothesized that higher tidal amplitudes, river discharge, temperature, direct rainfall and decreased potential evapotranspiration explain observed high mangrove AGB. Location. Neotropics and a small portion of the Nearctic region. Methods. A universal forest model based on site-level forest structure statistics was validated to spatially interpolate estimates of mangrove biomass at different locations. Linear models were then used to predict mangrove AGB across the Neotropics. Results. The universal forest site-level model was effective in estimating mangrove AGB using pre-existing mangrove forest structure inventories to validate the model. We confirmed our hypothesis that at continental scales higher tidal amplitudes contributed to high forest biomass associated with high temperature and rainfall, and low potential evapotranspiration. Our model explained 20% of the spatial variability in mangrove AGB, with values ranging from 16.6 to 627.0 t ha^{-1} (mean, 88.7 t ha^{-1}). Our findings show that mangrove AGB has been overestimated by 25–50% in the Neotropics, underscoring a commensurate bias in current published global estimates using site-level information. Main conclusions. Our analysis show how the ESH significantly explains spatial variability in mangrove AGB at hemispheric scales. This finding is critical to improve and explain site-level estimates of mangrove AGB that are currently used to determine the relative contribution of mangrove wetlands to global carbon budgets. Due to the lack of a conceptual framework explicitly linking environmental drivers and mangrove AGB values during model validation, previous works have significantly overestimated mangrove AGB; our novel approach improved these assessments. In addition, our framework can potentially be applied to other forest-dominated ecosystems by allowing the retrieval of extensive databases at local levels to generate more robust statistical predictive models to estimate continental-scale biomass values.

2.2 INTRODUCTION

Due to the large spatial extent and global distribution of mangroves along tropical and subtropical coastlines (Giri et al., 2011), these forested wetlands provide a wealth of ecosystem services to coastal communities and industries (Lee et al., 2014). Recent studies show that, at estimated rates, mangrove carbon (C) storage and sequestration are among the most important ecosystem services, given their potential economic value in global carbon markets to regulate carbon emissions in the context of climate change (Bouillon et al., 2008; Costanza et al., 2014). However, before assigning an economic value to this eco- system service at the global scale, it is critical to obtain accurate estimates of mangrove biomass (above- and belowground) and C stocks (Alongi, 2014).

Aboveground biomass (AGB) represents a significant portion of the total (vegetation and soils) organic carbon reservoir in mangrove forests (Lugo & Snedaker, 1974). Traditional summa- tion approaches to the estimation of AGB consider the incremental growth of trees and the productivity of canopy litterfall contributing to soil formation over time (Twilley et al., 1992; Rivera-Monroy et al., 2013). Further, the variation in annual carbon storage in biomass is a function of the climatic regime coupled with distinct geophysical and geomorphological variables (Twilley & Rivera-Monroy, 2009). Overall, mangrove net primary productivity (NPP) and biomass accumulation are high in coastal regions where a wide tidal range and high runoff, rainfall and nutrient inputs are present, in contrast to harsh environments (i.e. low temperatures and rainfall, periodical droughts, hypersalinity) where forest biomass is significantly lower (Schaeffer-Novelli et al., 1990; Twilley, 1995). The close relationship between these environmental drivers and mangrove NPP and biomass productivity has seldom been directly tested; consequently, predictions about the capacity of mangrove dominated-ecosystems to store carbon in AGB have been based on assumed relationships between their spatial distribution and latitudinal gradients (Twilley et al., 1992; Saenger & Snedaker, 1993).

The ability to estimate global mangrove AGB is limited by the validity and precision of models on different spatial scales, as exemplified by the use of site-specific allometric models and the

intrinsic variation in tropical and subtropical coastal environments. The development of these models depends primarily on sample size, which in turn requires extensive data collection and processing that is often limited by cost, time and logistics. These limitations result in reduced data availability generally associated with a geographical sampling bias (i.e. an uneven distribution of sampling efforts) that constrains the accuracy of estimates of global AGB (Sifleet et al., 2011). Consequently, recent estimates of global mangrove AGB are widely biased, due to an insufficient sample size of mangrove forest structural variables at the site level and lack of consideration of the significance of climate variables that are critical for predicting spatial pat- terns in mangrove biomass at continental scales (Hutchison et al., 2014). Other approaches have converted means values of mangrove biomass to latitudinal and longitudinal classes to extrapolate known site-level biomass measurements to a global scale (Twilley et al., 1992; Saenger & Snedaker, 1993). The combination of models necessary to scale variability in mangrove AGB from individual sites to continental scales has not yet been systematically tested.

We developed a set of statistical models to extrapolate estimates of site-level mangrove AGB using forest structural attributes to build a continental model to predict AGB in the Neotropics. To test our approach we used published and unpublished forest structural data throughout the Americas, where 26% of the world's mangroves are currently located (Giri et al., 2011), encompassing 60° in latitude and 90° in longitude. First, we describe a model to predict mangrove AGB at the site level (community) that uses existing forest structure inventories (summaries), allowing significant coverage of mangrove sites across distinct Neotropical coastal landforms. The ability to use estimates of AGB from a large number of coastlines facilitated the development of a robust continental-level model to predict mangrove AGB. Here, we built upon the framework of the environmental signature hypothesis (ESH), which states that geophysical forces in coastal settings, along with regional climate, control the structure (e.g. tree height) and function (e.g. NPP) of tropical coastal ecosystems (Twilley, 1995). We hypothesized that higher tidal amplitudes, river discharge regimes, temperature, rainfall and decreased potential evapotranspiration control high mangrove AGB across coastal landforms. Finally, we contrasted our results with observed values for mangrove AGB using previous latitude- (Twilley etal., 1992; Saenger & Snedaker, 1993) and climate-based models (Hutchison et al., 2014). Our results provide scientists and decision makers with more accurate tools for estimating and assessing

mangrove AGB, thus improving the analysis of global carbon budgets by using information at both site and continental scales.

2.3 METHODS

2.3.1 Model for estimating site-level mangrove AGB

A site-level AGB model based on forest structure data was developed to expand biomass estimates for a number of Neotropical mangrove sites. We used a universal forestry model that estimates AGB values from published forest inventories and is widely applied to forested ecosystems (Cannell, 1984) other than mangrove forests. Thus, AGB values estimated using this universal model were used to build an AGB database for a wide range of mangrove locations throughout the Neotropics. Values obtained with the universal model are denoted henceforth as estimated AGB values or universal model estimates.

Cannell's model is described by the following equation:

$$AGB = F \times (BA \times H) \times WSG \tag{1}$$

where F is a form factor, which is the ratio of the volume of a tree to the volume of a cylinder having the same length and cross-section as the tree (for a detailed description see Gray, 1956; Cannell, 1984), BA is basal area (m^2 ha^{-1}), H is height (m) and WSG is wood specific gravity (g dry mass cm^{-3}) (see Appendix S1 in Supporting Information for details).

The applicability of Cannell's universal model to mangrove forests was assessed using a global dataset (containing only peer-reviewed publications) comprising information on both published mangrove AGB values (either from harvested trees or a variety of different allometric models) and forest structure data (see Appendix 1 and Appendix S1). To validate Cannell's universal model for mangrove forests we used null model analysis (Gotelli & Graves, 1996) (see Appendix S1 for details).

Considering that both the estimates of AGB using the universal model (based on Cannell's model) and the published AGB values (based on data from either harvested trees or a variety of different allometric models) are both based on ground truth data collection (i.e. diameter at breast height [d.b.h.] and H), we used these forest structural attributes in our continental-scale analysis without distinction and refer to this data set hereafter as observed AGB or simply as observed.

2.3.2 Model for estimating continental-scale mangrove AGB

To develop the continental-scale model we used observed AGB values available for the Neotropics (see Appendix 1 for a full list of both published and unpublished studies used in modelling continental-scale AGB, and Appendix S2). We also used mangrove AGB data from locations lacking this information including the Pacific coast of Colombia and Ecuador (M. Simard, unpublished data) and Port Fourchon, LA, USA (A. A. Williams, unpublished data). When applying Cannell's model, we avoided using data from both naturally (stands subjected to hypersalinity, hurricanes) and human disturbed (timber extraction, impoundments) sites since tree architecture in those forests might lack allometric relationships (Chave et al., 2005, 2015; Soares & Schaeffer-Novelli, 2005). However, published AGB values from stunted (i.e. scrub) stands obtained from site-specific allometric models were included in the data set. Further, we did not include studies that relied solely on remote sensing data due to potential errors and uncertainty estimates related to the assessment of canopy height; overall, AGB model predictions from remote sensing information are inherently higher in some cases than AGB values obtained from field surveys based on d.b.h. (Hutchison et al., 2014, and references therein).

The geographical area (mask) used to model mangrove AGB in the Neotropics was obtained from a global distribution raster for mangrove forests derived from earth observation satellite imagery (Giri etal., 2011). To maximize the relationship between cell size and the quantity of available data (i.e. dependent and independent variables) (Blackburn & Gaston, 2002) the size of the degree cells used in our analysis was 0.25 (25 km2 at the equator). To adequately represent the spatial distribution of mangrove AGB, the third quartile was obtained from all the values within each 0.25° cell. This descriptive statistic was preferred over the mean (or the median) because it is less affected by outliers, particularly when distributions have a negative skew (Zar, 2010). For example, mangrove forest inventories in the Neotropics often include individual trees that are either > 1 m or have a d.b.h. > 2.5 cm. This selection of tree height and d.b.h. in the Neotropics is in contrast to assessments performed in other regions where higher d.b.h. values are included as a minimum value (usually > 10 cm). Thus, the rationale for opting for this descriptive statistic is that small trees can dominate the structural signal in a plot, thus underestimating the final AGB value when plots are averaged in a particular site. Additionally, this grouping

reduced bias due to differences in sampling efforts, and integrated the results of independent studies within the same grid cells. Different climatic and geophysical variables measured in those cells were used to test the best combination of regressors for the observed AGB values. We then used this continental-scale model to predict mangrove AGB in all grid cells along the Neotropical coastal zone.

The environmental variables used in our analyses were pre-selected based on the assumptions underlying the ESH hypothesis, which states that geophysical forces (tidal range, river discharge) in coastal settings, along with regional climate (air temperature, rainfall and evapotranspiration), control the structure and function of tropical coastal ecosystems (Thom, 1982; Twilley, 1995). Thus, the environmental variables included in our analysis were: (1) minimum temperature of the coldest month (Tmin, °C), (2) precipitation of the driest month (Pmin, mm year^{-1}), (3) potential evapotranspiration (PET, mm year^{-1}), (4) growing degree-days (GDD), (5) tidal range (TR, cm), and (6) river discharge (RD, m^3 s^{-1}) (see Appendix S3 for details). These variables were then tested for autocorrelation (Spearman's rank) and multicollinearity (variance inflation factor, VIF). Multiple regression (ordinary least squares, OLS) was used to assess the effect of environmental drivers on patterns of mangrove AGB in the Neotropics. Continental-scale models were evaluated based on the Akaike information criterion (AIC; Appendix S3). Also, we considered the relative importance of the model's terms (R^2 partition; Groemping, 2006). Statistical tests were run on untransformed data, except on the OLS regressions where AGB values were log transformed [$\ln(x + 1)$] to improve the model fit. Model performance was evaluated by residual analysis, and lack of fit was verified with pure error analysis. Pairwise Wilcoxon rank sum tests were used to compare model outputs given the skewed distribution of the data (Shapiro–Wilk test) and heteroscedasticity (Cochran's test). All statistical analyses including raster manipulations were performed using R statistical software (see Appendix S4 for details).

2.4 RESULTS

2.4.1 Site-level mangrove AGB estimates

Validation of Cannell's universal model for mangrove forests was performed using a global dataset that included sites representing a wide variety of coastal landforms (e.g. karstic versus deltaic) and associated mangrove ecotypes (e.g. riverine, fringe, basin) (Appendix S1). We identified 53 published studies reporting both mangrove AGB and forest structure data from 136 sites distributed world-wide. Cannell's universal model proved an effective estimator of mangrove AGB using site-level forest structural attributes. Figure 1 shows the frequency of 999 random simulated AGB differences (or simulated AGB_{diff}) obtained by subtracting published AGB values (AGB_{pub}) from AGB estimates using Cannell's model (AGB_{Cann}), i.e. simulated AGB_{diff} = simulated AGB_{pub} − simulated AGB_{Cann}. The actual observed AGB differences (in contrast to simulated values) represented by the centred solid line (approximately -7 t ha^{-1}) in relation to lower (-29 t ha^{-1}) and upper (27 t ha^{-1}) 95% confidence intervals (dotted lines) confirmed that there are no statistically significant differences ($\alpha > 0.05$) between published AGB values and those values estimated using Cannell's model.

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Figure 1 – The validation of Cannell's universal model for mangrove forests
was performed using a global dataset containing information on both published
mangrove aboveground biomass (AGB, in t ha^{-1}) (either from harvested trees or
a variety of different allometric models) and forest structure data (for details see
Table S2-1, Appendix S2). The histogram depicts the frequency distribution of
999 random simulated AGB differences (or simulated AGB_{diff}) obtained from
subtracting published AGB values (AGB_{pub}) from AGB estimated using
Cannell's model (AGB_{Cann}) (AGB_{diff} = simulated AGB_{pub} – simulated AGB_{Cann}).
The actual observed AGB differences (solid vertical line), and the lower and the
upper 95% confidence intervals (vertical dashed lines) confirm the null
hypothesis that there are no significant differences ($P = 0.34$) between published
and estimated AGB values using Cannell's model.
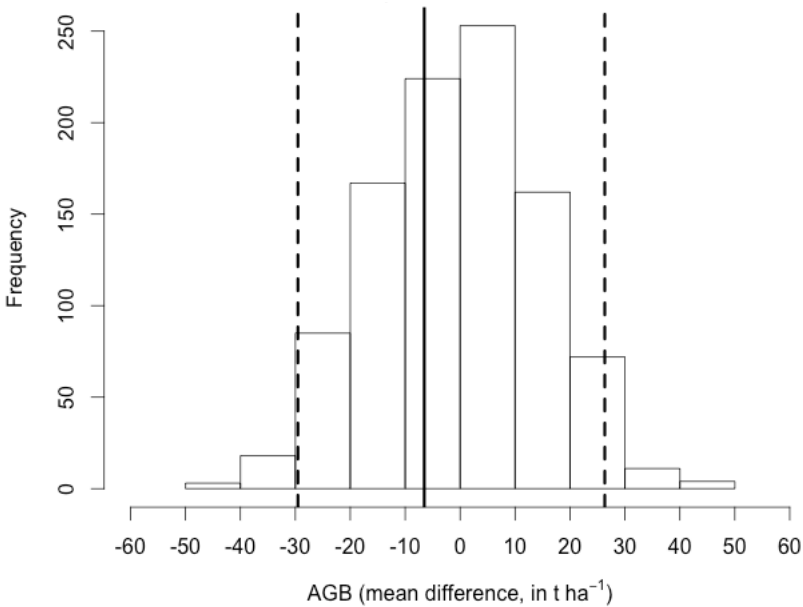
2.4.2 Continental-scale estimates of mangrove AGB

The literature review yielded a total of 175 studies reporting mangrove forest structure and AGB in the Neotropics, including a total of 1480 sites. After using the criteria to select sites to be included in our analyses (i.e. excluding data from disturbed sites or based on remote sensing), the final number of studies was 134 encompassing 1047 sites (Appendix S2). After aggregating sites into 0.25° cells, this dataset produced 135 AGB values (Fig. 2); this was the sample size used in our regression analyses.

Figure 2 – Distribution of observed values for mangrove aboveground biomass (AGB) (published and estimated using a site-level universal model; Cannell, 1984) included in the modelling analyses (n = 135). The data points on the map are consolidated into 0.25° cells representing 1047 sites and obtained from 134 independent studies.
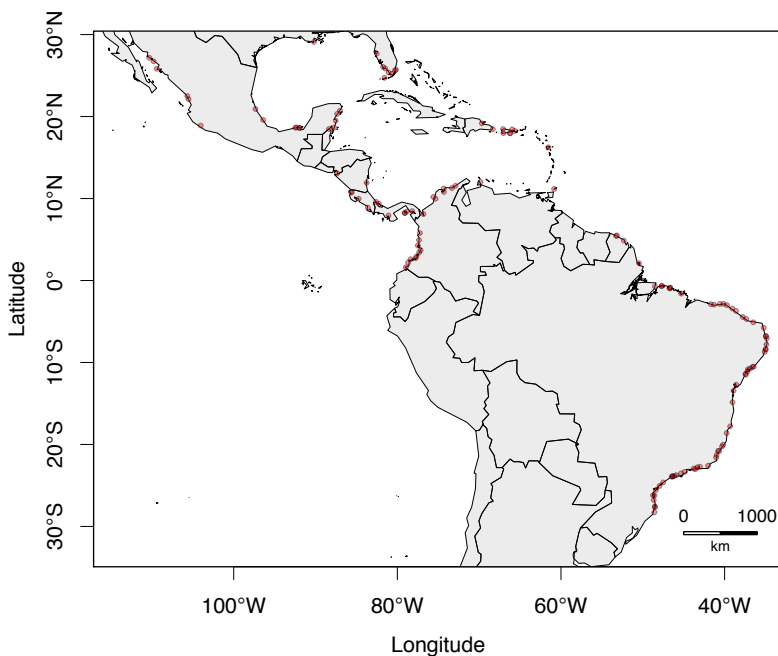
The GDD variable was highly correlated with Tmin ($r^2 = 0.89$; VIF = 7.83^{13}) and thereby it was removed from the analysis. The variables further considered in our analyses included Tmin, Pmin, PET,

TR and RD. The linear correlation coefficients of the remaining variables ranged from −0.02 (PET - Tmin) to 0.36 (TR - Tmin), while the VIF ranged from 1.06 (RD) to 1.24 (Tmin), indicating no multicollinearity. A global model was set up taking into consideration ecologically plausible interactions between environmental variables and mangrove AGB (i.e., the combined effects of temperature, precipitation and evapotranspiration results in the balance of moisture in terrestrial and coastal ecosystems). Then, the modelling approach involved OLS multiple regression and selection of the model with the best combination of variables.

The multimodel inference approach produced 13 models (out of 76 possible combinations) with ΔAIC values ranging from 0 to 7 (Appendix S5). The best-fitting model considered the lowest ΔAIC value as well as the frequency with which significant terms ($\alpha < 0.05$) were selected during model analyses. Regarding the relative importance of the model terms, Tmin:Pmin accounted for 34.05% of the the variability of the fitted model, followed by Tmin (18.96%), Pmin:PET (18.44%), PET (16.72%), TR (8.19%) and Pmin (3.63%). Finally, we also considered the model's absence of lack of fit ($P = 0.18$). Thus, the equation used to predict AGB over the area of mangroves in the Neotropics (Fig. 3a) was:

$$
\begin{aligned}
AGB(tha{-}1)=\exp\{&9.026+(-0.064Pmin)+(-0.067Tmin)\\
&+(-0.002PET)+(0.001TR)\\
&+[0.002(Tmin\times Pmin)]\\
&+[1.365{-}5(Pmin\times PET)]{-}1\}
\end{aligned} \tag{2}
$$

Our model explained approximately 20% of the spatial variability in mangrove AGB in the Neotropics (global R = 0.23, adjusted R^2 = 0.19, d.f. = 119, $P < 0.000$) with values ranging from 16.6 to 627.0 t ha^{-1} (mean 88.7 t ha^{-1}) (Fig. 3a). A quantitative comparison of our model output with other published climate- (Hutchison et al., 2014) (Fig. 3b) and latitude-based (Twilley etal., 1992; Saenger & Snedaker, 1993) (Fig.3c,d) models showed a significant difference in mangrove AGB values (see Appendix S6 for larger, high-resolution maps). Our model predicted mangrove AGB values similar to those directly measured (site-level field measurements) in the Neotropics (Fig. 3e). In contrast, climate- and latitude-based models overestimated mangrove AGB by 25.3% (Hutchison et al., 2014), 34.3% (Saenger & Snedaker, 1993) and 44.4% (Twilley et al., 1992) in the Neotropics.

Figure 3 – Prediction of mangrove aboveground biomass (AGB, in t ha−1) in the Neotropics using (a) a climatic–geophysical model, (b) Hutchison et al.'s (2014) climate-based model, (c) Saenger & Snedaker (1993) and (d) Twilley et al.'s (1992) latitude-based models. The box-plot (e) shows the differences between observed and modelled AGB values using currently available published and unpublished data throughout the Neotropics (see also Fig. 2). The climatic–geophysical model predicts AGB values similar to those observed, while other models show an overestimation. OB, observed; CG, climatic–geophysical model; HT, climate-based model (Hutchison et al., 2014); SS, latitude-based model (Saenger & Snedaker, 1993); TW, latitude-based model (Twilley et al., 1992). Samples size (n) = 135.
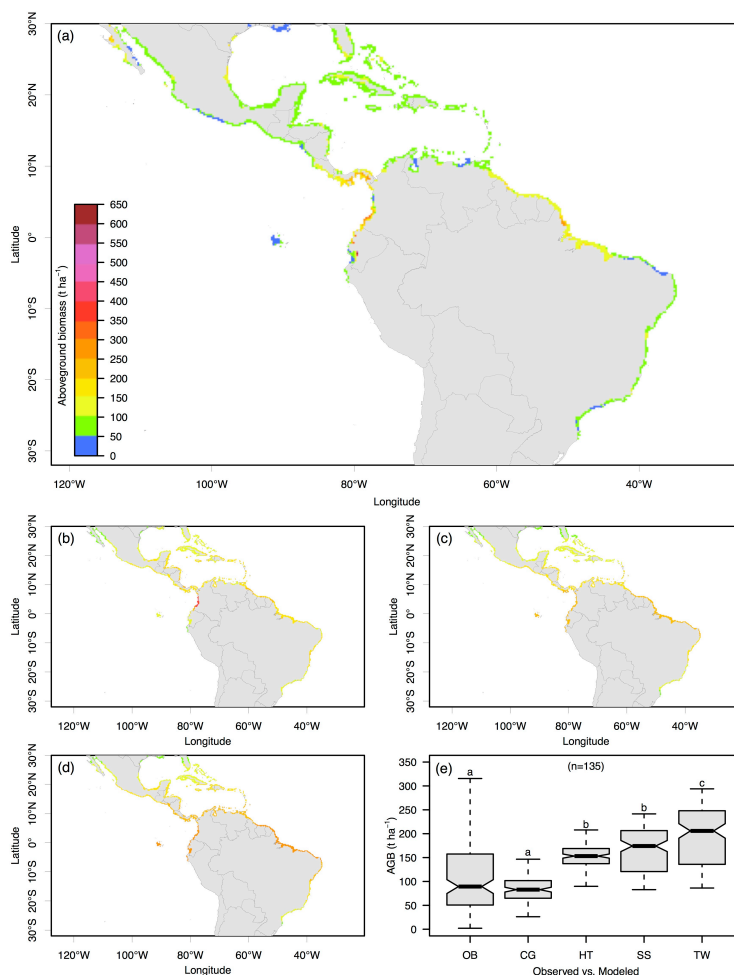
2.5 DISCUSSION

2.5.1 Site-level model of mangrove AGB

Our continental-level analyses benefited from the use of a large dataset obtained by converting site-level forest structure data into AGB values. We demonstrated that Cannell's model (Cannell, 1984) produced accurate AGB estimates for a wide array of mangrove habitats (Lugo & Snedaker, 1974; Thom, 1982). This forest model is thus a powerful tool for scaling up mangrove AGB from currently available forest structure datasets. The analytical approach provided here should minimize sample size constraints, improving model performance, predictive capability and enhancing the intrinsic fine-scale variability commonly observed in mangrove-dominated coastlines.

Cannell's model differs from other allometric models in its mathematical simplicity and applicability since only two easily sampled and commonly reported forest structural attributes (i.e. basal area and height) are required to estimate AGB values. Additionally, basal area at the site-level (m^2 ha^{-1}) is considered a better predictor of AGB than d.b.h. (Twilley & Rivera-Monroy, 2009), and because the model incorporates values at the forest stand level, AGB estimates are not constrained to any given diameter range. Further, because of the larger sample size used to derive forest inventory statistics (i.e. average from trees within a plot and across plots), the sampling error inherently present while acquiring tree-level data to construct allometric models is reduced at the stand-level (Chave et al., 2004). Finally, caution must be exercised when including sampling data from disturbed sites (i.e. illegally harvested and hypersaline sites) where tree architecture may depart from commonly observed allometric relationships (Chave et al., 2005; Soares & Schaeffer-Novelli, 2005).

Our review of mangrove forest structure and AGB data in the Neotropics also highlights gaps in research and methodology. For example, a number of studies either did not include or improperly reported forest structure variables. BA and average tree height are critical variables used to estimate AGB at site level, and should preferably be reported in m^2 ha^{-1} and m, respectively, to facilitate comparison among stands and sites. Similarly, the quadratic mean diameter (in cm) should be preferred over the mean stand diameter (Cintrón & Schaeffer-Novelli, 1984; Curtis & Marshall, 2000), whereas tree density should be reported in stems per hectare. Although the quadratic mean diameter and tree density are not essential for estimating AGB, they allow the calculation of BA (and vice versa) given their

direct relationship. We suggest that these variables are included in mangrove forest structure studies, not only to improve our understanding of the processes regulating structural development and productivity of forests across sites, but also regeneration dynamics and conservation status.

2.5.2 Continental-level model of mangrove AGB

Our results support the ESH proposed for mangrove-dominated ecosystems, suggesting that AGB allocation at the continental scale is not only dependent on climatic variables but also on local and regional geophysical forcings such as tidal amplitude, which was positively related to forest biomass. Our findings are ecologically significant since current published models for estimating AGB do not include or test the relative contribution of these variables in explaining the spatial distribution of mangrove AGB. Further, our model is composed of a set of environmental drivers that are ecologically meaningful and closely associated with observed spatial distribution patterns of AGB at larger geographical scales; thus it could potentially be applied to other continental coastal regions world-wide. Additionally, our continental-level model estimates can be used as a reference to compare mean global-level values obtained with other approaches including remote sensing analysis (e.g. Simard et al., 2006; Fatoyinbo & Simard, 2013) and spatially explicit dynamics models (e.g. Berger et al., 2008) since our model validation includes extensive and independently collected ground truth data.

Although river discharge (RD) was not selected as a significant driver in our analyses, it is undisputed that this variable has a major direct and indirect influence on soil resource and stressor gradients that regulate mangrove biomass allocation at regional and local scales (Castañeda-Moya et al., 2013). For example, riverine mangroves are characterized by optimum structural development (tall canopy height, higher AGB values) as a result of high nutrient availability and reduced soil salinity levels, which are strongly regulated by RD (Cintrón et al., 1978; Castañeda-Moya et al., 2006). Given the well-known interaction between freshwater input into mangrove coastlines and mangrove biomass, our study underscores the critical importance of selecting spatial scales (from m^2 and ha to km^2) when assessing the functional attributes of mangroves such as AGB. Indeed, the low observed RD (predictor) score in our statistical analysis is not only explained by its scale dependence, where it becomes more or less important depending on the size of the area included in the analysis, but also by the

interaction between cell size and the quantity and quality of available data (Blackburn & Gaston, 2002). Although the RD raster used in our analysis is an accurate measure of the integrated terrestrial runoff, the data do not account for the spatial variability (regional, local) in runoff distribution across the watershed (Fekete et al., 2002) or the net sediment input into the plots used to estimate biomass in each grid.

The most significant drivers explaining AGB values in our model were Tmin as well as its interaction with PET. Similarly, the interaction of Pmin with PET, as well as PET alone, were statistically significant. PET is essentially dependent on the net amount of solar energy reaching the forest canopy, thus controlling forest water balance, which in turn is considered to be a productivity metric representing the energy available for plants to convert into biomass (Holdridge, 1967; Evans et al., 2005). This energy source represents a major constraint on the spatial distribution and realized maximum biomass of mangrove wetlands, particularly considering the diversity of environmental settings and associated eco-geomorphic dynamics of mangroves (Thom, 1982; Woodroffe, 1992; Twilley, 1995). This dynamic change is strongly influenced by the local tidal range, a critical geophysical variable explaining a significant percentage of the total variance in AGB in our analysis. Indeed, tidal amplitude, a component of the hydroperiod regime in coastal regions, significantly influences the structural development of mangroves by promoting nutrient exchange and aeration of soil layers, which reduces the accumulation of sulphides, allowing higher growth rates and forest development (Lugo & Snedaker, 1974; Castañeda-Moya et al., 2013).

Previous attempts to predict continental-scale mangrove AGB include latitude- (Twilley et al., 1992; Saenger & Snedaker, 1993) and climate-based models (Hutchison et al., 2014). Although latitude-based models can indirectly encompass critical climatic and geophysical variables, their individual contribution to explaining the spatial patterns in AGB values is unknown since their explanatory power is not explicitly weighted in the statistical analysis. Although a climatic modelling approach explicitly includes climate variables such as temperature (mean temperature of the warmest and coldest quarters) and precipitation (precipitation of the wettest and driest quarters) to explain mangrove AGB at the global scale (Hutchison et al., 2014), this analysis is limited not only by the number of climatic variables included the model but also by the lack of other environmental variables that directly influence the structural and functional properties of mangroves at regional and local scales (Twilley, 1995; Twilley & Rivera-Monroy,

2009). The inclusion of other geophysical variables in our climatic–geophysical model significantly improves estimates of AGB at the latitudinal scale, as shown by the model validation.

Our analysis of current published data on AGB at specific sites in both the Neotropics and Old World and the use of these data sets to estimate AGB values across different Neotropical latitudes also underscores the bias generally found in current estimates of global AGB. This bias is based on the historical selection of study sites, mostly representing forests with typically high AGB values (e.g. riverine, fringe), and the absence data from forest of lower stature (e.g. basin, scrub) and consequently low AGB values. This selective sampling, perhaps due to logistical accessibility for sampling, has skewed the distribution frequency of AGB values generally used in published work, since most of the authors used the same information to develop their statistical models (but see Saenger & Snedaker, 1993). For example, Twilley et al. (1992) reported a range of AGB values from 104.2 t ha^{-1} (high tropics) to 283.6 t ha^{-1} (low tropics), with a mean value of 178.2 t ha^{-1}. Using practically the same data set, Saenger & Snedaker (1993) reported mangrove AGB values ranging from 6.8 t ha^{-1} to 436.4 t ha^{-1} (low and high latitudes, respectively). Despite this original sampling bias in the representation of a wide range of ecotypes (i.e. AGB values) found at the same latitude, current mangrove AGB models do not consider this skewness to avoid such bias in the estimation, extrapolation and ecological interpretation of AGB values at the global scale (e.g. Siikamäki et al., 2012; Hutchison et al., 2014). For example, the most recent average AGB value reported for the Neotropics using a climate-based model was 165.5 t ha^{-1} (Hutchison et al., 2014). Fitting this model to our data set coordinates (Fig. 2) we obtained an average value of 153.1 t ha^{-1}, which is higher than the observed (89.3 t ha^{-1}) and estimated (82.9 t ha^{-1}) values using our climatic–geophysical model. The difference in model output (54%) is not only related to the type and number of variables included in our continental-scale model, but also to the sample size and spatial coverage used to produce the model. Further, predictions beyond the range of values used to construct each model might also contribute to differences in output (Saenger & Snedaker, 1993).

Nevertheless, the overall explanatory power of both our climatic–geophysical model and the climate-based model (Hutchison et al., 2014) is within less than 30% of the observed latitudinal variance in AGB. Although differences in model results could be explained by the use of different data sets during model development and validation, as well as

the actual areal extent included in the analysis (Neotropics versus global), it is clear that there are other variables and interactions that contribute to the variability in AGB at local and regional scales (Lugo & Snedaker, 1974; Thom, 1982). Regionally, physical properties of landforms together with the relative influence of rainfall, river discharge, tidal amplitude, turbidity and wave energy control the structural and functional patterns of mangroves (Woodroffe, 1992; Twilley, 1995). These regional ecogeomorphic differences (from hectare to km^2) can be further separated into local mangrove ecotypes (sensu Lugo & Snedaker, 1974) where microtopography (from m^2 to ha) drives the availability and limitation of resources (nutrients, light, space), regulators (salinity, sulphide, pH, redox) and hydroperiod (depth, frequency and duration of inundation) (Castañeda-Moya et al., 2013). This interaction at lower spatial scales determines not only species-specific spatial distribution of mangroves (Crase et al., 2013), but also patterns of allocation of both AGB and belowground biomass (Castañeda-Moya et al., 2013). Hence, within the ESH framework, we propose that the variance in AGB unaccounted for in our model can be explained by the interaction of regional and local drivers where low and high AGB values are present at the same latitude depending on the magnitude of such interaction (Twilley et al., 1992).

Due to the spatial scale at which climate variability and change occur, our continental-scale modelling approach can capture potential changes in the functional properties of mangrove (e.g. biomass, NPP) spatial distribution that may be induced by future climate change. Indeed, rising air temperatures are not only expected to increase mangrove NPP but also to trigger changes in the spatial distribution of AGB as future climate scenarios project the poleward expansion of mangrove species (Cavanaugh et al., 2015). A significant decrease in regional rainfall will reduce surface and subsurface inputs of freshwater, increasing both the interstitial salinity of soils and sulphide concentrations, which in turn will constrain mangrove growth (Snedaker, 1995). In contrast, in areas where an increase in rainfall is expected water availability could enhance growth and development of mangrove wetlands as a result of higher nutrient and water turnover rates lowering the effect of anoxic conditions (Field, 1995; Gilman et al., 2008). PET, a good proxy for estimating evapotranspiration, represents a standardized value in different climatic conditions facilitating comparative analyses of different evaporative environments (Asadi-Zarch et al., 2015), particularly in arid and semi-arid zones where scrub and basin mangroves are dominant (Cintrón et al., 1978;

Castañeda-Moya et al., 2006). Shifts in PET associated with climate change may preferentially affect interior mangrove zones by increasing soil salinity (Twilley & Chen, 1998). The direct impact of climate change on global tidal regimes is unclear, yet it is likely that sea level rise will affect tidal dynamics (hydroperiod) in coastal wetlands by controlling the relative impact of both net freshwater runoff and sediment discharge and redistribution at the regional geomorphic scale (Alongi, 2008; Gilman et al., 2008; Müller et al., 2011; Pelling et al., 2013).

Our comparative analysis shows that mangrove AGB has been overestimated by 25–50% in the Neotropics, indicating a com-mensurate bias in global estimates of AGB. This finding is critical, since mangrove carbon budgets rely on the estimation of AGB as a prior step in the estimation of both ecosystem-level carbon budgets and economic value. Once total carbon (above- and belowground) in mangrove wetlands has been estimated, these values are used as a proxy to determine CO^2 emissions, assuming all carbon stored is lost as result of land conversion (Howard et al., 2014). Our modelling approach is closely related to the tier system used by the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2013). In their three-tier scheme, accuracy increases from the use of default published values carrying a ± 50% error range (tier 1), and country or site-specific assessments (tier 2), to highly specific data sets that include several ecosystem components, including repeated measures (tier 3). Here we provide a framework to scale up continental-scale mangrove AGB from pre-existing site-level inventories (tiers 2 and 3). While current assessments are mostly grounded on the mean carbon values of an ecosystem (i.e. IPCC's tier 1; see Twilley et al., 1992; Siikamäki et al., 2012; IPCC, 2013), our approach advances techniques for estimating continental-scale mangrove carbon to higher tiers of detail, thus meeting international standards such as those outlined by the IPCC (tiers 2 and 3) and REDD+ programmes.

2.6 CONCLUSIONS

In this study we have proposed a novel modelling approach to scale up mangrove AGB to the continental level from currently available (published and unpublished) site-level forest structural data. Our approach differs from previous studies in three aspects. First, we used a set of statistical models to produce site-level mangrove AGB values using forest structural variables to build a regression-based model to

predict continental-level AGB values in the Neotropics. Mining of mangrove structural data to increase the sample size of currently available AGB values improved the predictive power of our continental-scale model. Second, our model included a set of ecologically meaningful environmental drivers, which were not included in previous published models, to explain the spatial patterns of AGB. Finally, we validated our model output against direct field measurements and comparatively determined the differences in site- specific or regional averaged AGB values predicted by different published models. Additionally, our analyses improve the estimation of AGB values in the Neotropics needed to produce mangrove carbon budgets within the highest accuracy recognized by international organizations (e.g. IPCC, REDD+ programmes).

2.7 ACKNOWLEDGEMENTS

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2.9 SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods: model for estimating site-level man- grove aboveground biomass.
Appendix S2 Methods: references used in the mangrove AGB continental-scale modelling analyses.
Appendix S3 Methods: variables used to develop a continental-scale mangrove AGB model.
Appendix S4 Methods: statistical routines and R packages algorithms.
Appendix S5 Results: regression parameters of the models evaluated.
Appendix S6 Results: larger, higher-definition maps used in Fig. 3(a–d).

2.10 BIOSKETCH

André Rovai is a marine ecologist interested in the ecology and restoration of coastal wetlands. His PhD focuses on regional and macroecological drivers and patterns of mangrove aboveground biomass and soil stoichiometry.

2.11 APPENDIX 1 DATA SOURCES

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Supporting Information – Appendix S1
Rovai et al. - Scaling mangrove aboveground biomass from site-level to continental-scale

APPENDIX S1

Methods - Model to estimate site-level mangrove aboveground biomass

Model variables

Cannell's model (Cannell, 1984) (eq. 1) estimates forest stand-level aboveground biomass using the following variables: basal area (BA, m^2 ha^{-1}), height (H, m), wood specific gravity (WSG, g dry mass per cm^3), and a stand form factor (F):

$$AGB = F \times (BA \times H) \times WSG \tag{1}$$

When BA data was lacking for a specific site in our metadata analysis, the following equation was used to estimate the missing value:

$$BA = k \times D \times (QSD)^2 \tag{2}$$

Equation 2 includes the interaction among BA, the quadratic mean diameter (QSD, cm) value, and tree density (D, number of trunks or stems per ha); k is a constant that depends on the measurement units originally used in the calculation (0.0000785 for QSD in cm; for details see Curtis & Marshall, 2000). Given that large differences between average (i.e., arithmetic mean) diameter at breast height (DBH) and QSD values are atypical (Curtis & Marshall, 2000), we indistinctly used these diameter descriptors in our analysis. The F variable is the ratio of the volume of a tree to the volume of a cylinder having both the same length and cross section as the original tree (for detailed description see Gray, 1956; Cannell, 1984). In this study we use a previously estimated value of F = 0.7 for mangrove wetlands (Roberts & Ruara, 1967; Kairo et al., 2002; Bundotich et al., 2009), which is within the range (0.6-0.8) estimated for other tropical broad-leaved forests (Gray, 1956; Cannell, 1984; Chave et al., 2005, 2015). An average WSG value of 0.77 was computed from the literature (Table S1-1) and includes information from the dominant mangrove species (sensu Thomlinson, 1986). Mean WSG values reported for a number of tropical trees (genus and family)

obtained either directly from field studies or from global databases do not differ, thus this information can be reliably used in allometric-based scaling up of tree biomass (Chave et al., 2015).

Validation of Cannell's model for mangrove forests

To validate the applicability of Cannell's universal model for mangrove forests we performed a literature review to assemble a dataset of published mangrove AGB and forest structure data. Literature searches were performed online using Scopus, ISI, Biological Abstracts, and Scielo websites. The keywords used in the search were "mangrove" plus "biomass", "aboveground biomass", "AGB", "carbon", "productivity", and "woody production". We retrieved 53 studies reporting both mangrove AGB (either from harvested trees or variety of allometric models) and forest structure data (Table S1-2). This data set includes measurements from 136 sites representing a broad biogeographic distribution (Ellison, 2002) and both diverse environmental settings (Thom, 1982; Woodroffe, 1992) and mangrove ecotypes (Lugo & Snedaker, 1974; Schaeffer-Novelli et al., 2000, 2005). If the environmental setting information was not explicitly included in the paper, we assigned it using Google Earth. Similarly, if the ecotype classification was not included, we assigned a category of "fringe" if the site was located within the first fifty meters from the water edge and "basin" if located beyond this distance threshold; in cases where it was not possible to assign a classification, the study was excluded from the analyses.

We validated the model output by randomly partitioning the dataset into subsets of observations to construct the model (70%) and to test (30%) the differences between observed versus estimated values. We built a linear model with the larger subset (i.e., 70% of data) to evaluate the relationship between published AGB values and calculated AGB model values (obtained using Cannell's model). Additionally, we tested the model by comparing the difference between published AGB and AGB estimated through Cannell's universal model using null model analysis (Gotelli & Graves, 1996). The probability of obtaining this observed difference between models by chance was compared with the simulated probabilities (999 randomizations) using an empirical cumulative distribution function.

Table S1-1. Mangrove species-specific wood densities (g/cm^3).

Element type*	Species	Source							3rd quartile
		1	2	3	4	5	6	7	
MJ	*Avicennia alba*	0.58	0.70					0.56 0.67 0.53	0.67
MJ	*Avicennia germinans*	0.87			0.66			0.90 0.79 0.75 0.67 0.77	0.83
MJ	*Avicennia intermedia*							0.64	0.64
MJ	*Avicennia marina*	0.88	0.69		0.66			0.52 0.69 0.65 0.73	0.71
MJ	*Avicennia nitida*							0.90	0.90
MJ	*Avicennia officinalis*				0.65			0.59 0.62	0.64
MJ	*Avicennia schaueriana*					0.73			0.73
MJ	*Avicennia tonduzii*							0.64	0.64
MJ	*Bruguiera cylindrica*	0.89		0.74				0.72	0.82
MJ	*Bruguiera exaristata*							0.84	0.84
MJ	*Bruguiera gymnorhiza*	0.97	0.50		0.74			0.84 0.76 0.66 0.80	0.82
MJ	*Bruguiera hainesii*							0.82	0.82
MJ	*Bruguiera parviflora*	0.93			0.83			0.74 0.78 0.80	0.83
MJ	*Bruguiera sexangula*	0.91			0.80			0.74	0.86
MJ	*Ceriops candolleana*							0.79	0.79
MJ	*Ceriops decandra*	1.07	0.69					1.07	1.07
MJ	*Ceriops tagal*	1.07	0.80	0.86				0.88 0.88 0.88 0.78 0.76	0.88
MJ	*Kandelia candel*				0.56			0.51 0.46 0.56	0.56
MJ	*Kandelia rheedei*							0.57	0.57
MJ	*Laguncularia racemosa*	0.76				0.93		0.60 0.62	0.80
MJ	*Lumnitzera littorea*							0.67 0.67 0.66 0.74	0.69
MJ	*Lumnitzera racemosa*	0.65						0.71	0.70
MJ	*Rhizophora apiculata*	0.90			1.05			0.85 0.84	0.94
MJ	*Rhizophora candelaria*							0.85	0.85
MJ	*Rhizophora mangle*	1.01			0.83	0.93		0.89 0.84 1.05 0.90 0.88 0.81 0.91	0.93
MJ	*Rhizophora mucronata*	1.13		0.77	0.87			0.77 0.82 0.74 0.84 0.90	0.88
MJ	*Rhizophora racemosa*				0.96		0.96	0.88 1.00 0.92	0.96
MJ	*Rhizophora stylosa*	0.90						0.84	0.89
MJ	*Rhizophora harrisonii*							0.84 0.88	0.87
MJ	*Sonneratia alba*	0.85		0.48	0.78			0.63 0.39	0.78
MJ	*Sonneratia apetala*	0.57	0.57		0.52			0.54 0.52	0.57

Element type*	Species	1	2	3	4	5	6	7	3rd quartile
MJ	*Sonneratia caseolaris*	0.70			0.55			0.39 0.39	0.59
MJ	*Sonneratia griffithii*							0.69	0.69
MJ	*Sonneratia ovata*							0.37	0.37
								Average MJ (±SE)	**0.77 (0.02)**
MI	*Aegialitis rotundifolia*				0.64				0.64
MI	*Aegiceras corniculatum*	0.70						0.51	0.65
MI	*Aegiceras floridum*							0.68	0.68
MI	*Camptostemon philippinense*							0.42	0.42
MI	*Excoecaria agallocha*	0.45						0.34 0.39 0.38 0.48 0.46 0.38	0.45
MI	*Heritiera fomes*	1.01						0.82	0.96
MI	*Heritiera littoralis*	0.89						0.77 0.79 1.04 0.95 0.69	0.94
MI	*Osbornia octodonta*							0.82	0.82
MI	*Pelliciera rhizophorae*							0.75	0.75
MI	*Pemphis acidula*							0.94	0.94
MI	*Pterocarpus officinalis*							0.41 0.36 0.28 0.30 0.43 0.45 0.42 0.41	0.42
MI	*Xylocarpus granatum*	0.80	0.62	0.60	0.70			0.56 0.53 0.62	0.66
MI	*Xylocarpus moluccensis*	0.80			0.67			0.61	0.74
								Average MI (±SE)	**0.70 (0.05)**

1. Saenger (2002); 2. Ray et al. (2012), 3. Komiyama et al. (2002); 4. Simpson (1996); 5. Medeiros & Sampaio (2008); 6. Adedeji et al. (2013); 7. Chave et al. (2009), Zanne et al. (2009); * MJ - major mangrove tree species; MI - minor mangrove tree species (sensu Tomlinson 1986).

Table S1-2. Global mangrove forest structure dataset used to validate Cannell's model (Cannell, 1984). AGB-aboveground biomass, BA-basal area, H-height, QSD-quadratic mean diameter, D-density.

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha^{-1})	BA (m^2 ha^{-1})	H (m)	QSD (cm)	D (st ha^{-1})	Reference
Saudi Arabia (Shuaiba)	38.292566	23.930317	3	Interior		*Avicennia marina*	18.58	22.77	3.00	16.70	1040	Abohassan et al. (2012)
Saudi Arabia (Yanbu)	38.194444	23.977666	2	Fringe		*Avicennia marina*	10.77	9.08	2.57	9.30	1337	Abohassan et al. (2012)
Sri Lanka	8.840000	6.210000	3	Fringe		*Avicennia marina*	240.00	43.80	7.20	26.40	1500	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.840000	6.210000	3	Fringe		*Avicennia marina*	193.00	29.70	10.30	29.00	738	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.840000	6.210000	3	Fringe		*Avicennia marina, Rhizophora mucronata, Lumnitzera racemosa*	172.00	34.30	4.30	16.87	3034	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.840000	6.210000	3	Fringe		*Avicennia marina, Rhizophora mucronata, Lumnitzera racemosa, Ceriops tagal*	85.00	19.99	4.40	8.41	4650	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.840000	6.210000	3	Fringe		*Avicennia marina, Rhizophora mucronata*	71.00	11.40	3.90	8.12	4650	Amarasinghe & Balasubramaniam (1992)
Sri Lanka	8.840000	6.210000	3	Fringe		*Avicennia marina, Rhizophora mucronata, Lumnitzera racemosa, Ceriops tagal*	57.00	13.10	4.50	7.79	5190	Amarasinghe & Balasubramaniam (1992)
Mozambique (Inhaca island)	32.914679	-26.036074	2	Fringe		*Avicennia marina, Ceriops tagal, Bruguiera cylindrica, Rhizophora mucronata*	107.00	19.44	2.20	6.40	6047	Boer (2000)
Kenya (Gazi Bay)	39.520000	-4.410000	2	Fringe	Natural forest	*Rhizophora mucronata*	452.02	34.00	7.50	11.62	2570	Bosire et al. (2003); Kirui et al. (2006)
USA (Shark River, Florida)	-80.964167	25.409722	2	Fringe	Natural forest	*Laguncularia racemosa, Rhizophora mangle, Conocarpus erecta*	108.00	23.50	6.00	6.22	7746	Castaneda-Moya et al. (2013)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha^{-1})	BA (m^2 ha^{-1})	H (m)	QSD (cm)	D (st ha^{-1})	Reference
USA (Shark River, Florida)	-81.032214	25.376873	2	Fringe	Natural forest	*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	95.40	22.30	8.30	9.99	2844	Castaneda-Moya et al. (2013)
USA (Shark River, Florida)	-81.077768	25.364407	2	Fringe	Natural forest	*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	162.20	40.90	13.00	13.55	2838	Castaneda-Moya et al. (2013)
USA (Taylor River, Florida)	-80.524441	25.232463	6	Scrub	Natural forest	*Rhizophora mangle*	4.40	1.30	3.20	3.97	1050	Castaneda-Moya et al. (2013)
USA (Shark River, Florida)	-81.050556	25.370000	2	Fringe	Natural forest	*Rhizophora mangle, Avicennia germinas, Laguncularia racemosa*	247.59	40.75	10.20	11.70	3793	Chen & Twilley (1999)
USA (Shark River, Florida)	-81.050556	25.370000	2	Fringe	Natural forest	*Rhizophora mangle, Avicennia germinas, Laguncularia racemosa*	251.85	40.00	9.90	11.80	3650	Chen & Twilley (1999)
USA (Shark River, Florida)	-81.050556	25.370000	2	Fringe	Natural forest	*Rhizophora mangle, Avicennia germinas, Laguncularia racemosa*	120.87	20.94	7.90	10.10	2635	Chen & Twilley (1999)
USA (Shark River, Florida)	-81.050556	25.370000	2	Fringe	Natural forest	*Rhizophora mangle, Laguncularia racemosa, Conocarpus erecta*	79.68	19.81	5.50	5.80	7395	Chen & Twilley (1999)
Brazil (Babitonga Bay)	-48.750720	-26.204539	2	Fringe		*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	37.20	17.08	3.50	6.97	6475	Cunha et al. (2006)
Mexico (Boca Chica)	-92.330000	18.670000	4	Fringe		*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle*	135.00	34.20	20.00	8.13	3360	Day-Jr et al. (1987)
Mexico (Estero Pargo)	-92.330000	18.670000	4	Fringe		*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle*	120.00	23.30	6.00	5.63	7510	Day-Jr et al. (1987)
French Guiana	-52.320000	4.870000	2	Fringe	Matured coastal	*L. racemosa, A. germinans, Rhizophora*	315.00	33.60	22.70	30.10	780	Fromard et al. (1998)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha⁻¹)	BA (m² ha⁻¹)	H (m)	QSD (cm)	D (st ha⁻¹)	Reference
French Guiana	-52.320000	4.870000	2	Fringe	Matured riverine	*Laguncularia racemosa, Avicennia germinans, Rhizophora*	188.60	24.00	23.00	32.10	3310	Fromard et al. (1998)
French Guiana	-53.250000	5.420000	2	Fringe	Matured coastal	*Laguncularia racemosa, Avicennia germinans, Rhizophora*	180.00	24.60	19.60	23.60	917	Fromard et al. (1998)
French Guiana	-53.250000	5.420000	2	Fringe	Matured riverine	*Rhizophora, Avicennia germinans, Pterocarpus oficinalis*	122.20	17.80	19.10	21.70	3167	Fromard et al. (1998)
French Guiana	-52.320000	4.870000	2	Fringe	Young stage	*Laguncularia racemosa, Avicennia germinans*	71.80	20.60	7.70	4.70	11944	Fromard et al. (1998)
French Guiana	-53.170000	5.500000	2	Fringe	Pioneer stage 1-year-old	*Rhizophora, Avicennia germinans, Laguncularia racemosa*	35.10	12.50	2.80	2.40	31111	Fromard et al. (1998)
French Guiana	-53.250000	5.420000	2	Fringe	Pioneer stage	*Laguncularia racemosa, Avicennia germinans*	31.50	13.70	3.50	2.10	41111	Fromard et al. (1998)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Pioneer mangrove	*Avicennia germinas, Laguncularia racemosa*	56.60	21.80	5.00	2.7	29000	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Pioneer mangrove	*Avicennia germinas, Laguncularia racemosa*	11.42	4.08	2.50	2.3	8400	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Young mangrove	*Avicennia germinas, Laguncularia racemosa*	61.40	21.40	5.00	4.3	9200	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Young mangrove	*Avicennia germinas, Laguncularia racemosa*	50.20	18.04	5.00	4.5	8400	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Young mangrove	*Avicennia germinas, Laguncularia racemosa*	73.10	18.03	5.50	4.8	8000	Fromard et al. (2004)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha⁻¹)	BA (m² ha⁻¹)	H (m)	QSD (cm)	D (st ha⁻¹)	Reference
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Young mangrove	*Avicennia germinas, Laguncularia racemosa*	32.39	8.60	5.00	4.3	5151	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Young mangrove	*Avicennia germinas, Laguncularia racemosa*	14.58	4.00	6.10	4.4	2400	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Adult mangrove	*Avicennia germinas, Rhizophora mangle, Rhizophora racemosa*	180.00	24.60	20.00	23.6	917	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Adult mangrove	*Avicennia germinas, Rhizophora mangle, Rhizophora racemosa*	214.40	22.50	22.00	44.90	663	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Adult mangrove	*Avicennia germinas, Rhizophora mangle, Rhizophora racemosa*	228.84	26.86	18.20	24.20	450	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Mature mangrove	*Avicennia germinas*	431.90	51.40	24.80	67.10	162	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Mixed mangrove	*Avicennia germinas*	122.20	17.81	19.00	21.70	3047	Fromard et al. (2004)
French Guiana (Sinnamary estuary)	-53.250000	5.416667	2	Fringe	Cemetery stand	*Avicennia germinas, Laguncularia racemosa*	110.00	18.50	15.00	28.50	267	Fromard et al. (2004)
French Guiana (Sinnamary est.)	-53.250000	5.416667	2	Fringe	Cemetery stand	*Avicennia germinas, Laguncularia racemosa*	77.60	13.80	17.00	31.10	825	Fromard et al. (2004)
Panama	-78.177725	8.463944	2	Fringe		*Rhizophora brevistyla*	279.40	13.56	41.00		712	Golley et al. (1969, 1975)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Fringe	Natural stand	*P. rhizophorea, R. racemosa*	105.70	24.70	8.52	8.12	8325	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Fringe	Natural stand	*P. rhizophorea, R. racemosa*	335.30	27.50	13.53	15.47	3675	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Fringe	Natural stand	*P. rhizophorea, R. racemosa*	110.80	16.70	12.13	14.40	1400	Gross et al. (2014)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha^{-1})	BA (m^2 ha^{-1})	H (m)	QSD (cm)	D (st ha^{-1})	Reference
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Interior	Natural stand	*Pelliciera rhizophorea, Rhizophora racemosa*	132.70	33.50	7.65	13.85	8025	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Interior	Natural stand	*Pelliciera rhizophorea, Rhizophora racemosa*	164.20	26.80	10.53	14.10	8400	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Interior	Natural stand	*Pelliciera rhizophorea, Rhizophora racemosa*	76.20	23.30	8.30	10.93	10500	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Interior	Natural stand	*Pelliciera rhizophorea, Rhizophora racemosa, Avicennia germinans*	248.70	27.70	8.30	10.43	3950	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Interior	Natural stand	*Pelliciera rhizophorea, Rhizophora racemosa, Avicennia germinans*	267.20	33.40	9.97	13.69	4475	Gross et al. (2014)
Panama (Gulf of Monitjo)	-81.077842	7.930253	2	Interior	Natural stand	*Pelliciera rhizophorea, Rhizophora racemosa, Avicennia germinans*	139.10	11.10	11.42	12.28	1100	Gross et al. (2014)
Japan (Manko Wetland, Okinawa)	127.680000	26.190000	2		14-years-old stand	*Kandelia obovata*	109.28	36.27	4.17	5.83	13588	Hoque et al. (2011)
Malaysia (Kuala Sepetang, Matang)	100.617006	4.836569	2	Interior	20-years-old plantation	*Rhizophora apiculata, Bruguiera gymnorrhiza*	214.32	29.34	21.00	12.40	2425	Jin-Eong et al. (1995)
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	180.00	33.10	11.00	14.60	1700	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	94.00	23.80	7.00	11.50	1200	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	215.00	30.20	12.50	9.00	4300	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	102.00	20.40	8.80	10.50	2100	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	118.00	21.60	10.50	10.10	2000	Juman (2005)
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	20.00	8.40	3.00	4.40	4200	Juman (2005)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha⁻¹)	BA (m² ha⁻¹)	H (m)	QSD (cm)	D (st ha⁻¹)	Reference
Tobago (Bon Accord Lagoon)	-60.824267	11.166505	3	Fringe		*Rhizophora mangle*	259.00	30.40	15.00	11.10	2900	Juman (2005)
Kenya (Gazi Bay)	39.520000	-4.410000	2	Fringe	12-years-old plantation	*Rhizophora mucronata, Ceriops tagal, Bruguiera gymnorrhiza, Xylocarpus granatum, Sonneratia alba*	106.70	17.12	8.37	6.30	5132	Kairo et al. (2008)
Kenya (Gazi Bay)	39.520000	-4.410000	2		8-years-old plantation	*Avicennia marina plantation*	11.70	13.69	5.30	7.50	3100	Kairo et al. (2009)
Kenya (Gazi Bay)	39.520000	-4.410000	2		5-years-old plantation	*Sonneratia alba plantation*	6.70	20.71	4.50	8.90	3330	Kairo et al. (2009)
Kenya (Gazi Bay)	39.520000	-4.410000	2		8-years-old plantation	*Ceriops tagal plantation*	3.70	6.33	2.30	5.10	3100	Kairo et al. (2009)
Kenya (Gazi Bay)	39.520000	-4.410000	2		5-years-old plantation	*Rhizophora mucronata plantation*	20.25	7.34	3.90	5.30	3330	Kairo et al. (2009); Kairo et al. (2001); Bosire et al. (2003, 2006)
Micronesia (Airai, Palau)	134.539178	7.352020	7	Fringe			174.00	35.00	5.68	11.58	3326	Kauffman et al. (2011)
Micronesia (Airai, Palau)	134.539462	7.352941	7	Interior			212.00	36.00	5.41	13.82	2400	Kauffman et al. (2011)
Micronesia (Airai, Palau)	134.539831	7.354299	7	Interior			289.00	43.00	6.48	19.07	1507	Kauffman et al. (2011)
Micronesia (Yap)	138.127499	9.588354	7	Fringe			251.00	42.00	7.07	28.69	650	Kauffman et al. (2011)
Micronesia (Yap)	138.127506	9.587323	7	Interior			456.00	78.00	7.05	40.69	600	Kauffman et al. (2011)
Micronesia (Yap)	138.127444	9.586271	7	Interior			383.00	65.00	6.96	27.65	1083	Kauffman et al. (2011)
Japan (Okinawa)	127.680000	26.190000	2	Fringe	10-years-old stand	*Kandelia obovata*	75.10	12.36	2.82	1.87	45000	Khan et al. (2004, 2007)
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Bruguiera gymnorrhiza forest*	436.40	35.90	22.40			Komiyama et al. (1988)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha^{-1})	BA (m^2 ha^{-1})	H (m)	QSD (cm)	D (st ha^{-1})	Reference
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Bruguiera gymnorrhiza forest*	406.60	36.20	26.40			Komiyama et al. (1988)
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Rhizophora apiculata forest*	356.80	25.10	21.20			Komiyama et al. (1988)
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Rhizophora apiculata forest*	299.10	22.80	15.50			Komiyama et al. (1988)
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Rhizophora stylosa forest*	178.20	14.00	22.30			Komiyama et al. (1988)
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Sonneratia forest*	169.10	21.20	15.90			Komiyama et al. (1988)
Indonesia (Halmahera)	128.490000	1.310000			Primary forest	*Rhizophora apiculata forest*	216.80	18.70	15.80			Komiyama et al. (1988)
Thailand (Satun Southern)	100.160000	6.590000	2	Fringe	Secondary forest	*Ceriops tagal, Rhizophora apiculata, Xylocarpus moluccensis*	92.20	15.20	5.20	4.20	11000	Komiyama et al. (2000)
Indonesia (East Sumatra)	103.802865	0.018566	1	Fringe		*Bruguiera parviflora stand*	89.68	9.20	18.80			Kusmana et al. (1992)
Indonesia (East Sumatra)	103.802865	0.018566	1	Fringe		*Bruguiera parviflora stand*	42.94	4.00	19.50			Kusmana et al. (1992)
Indonesia (East Sumatra)	103.802865	0.018566	1	Fringe		*Bruguiera sexangula stand*	75.99	5.00	17.10			Kusmana et al. (1992)
Indonesia (East Sumatra)	103.802865	0.018566	1	Interior		*Bruguiera sexangula stand*	178.81	15.20	20.10			Kusmana et al. (1992)
Indonesia (East Sumatra)	103.802865	0.018566	1	Interior		*Bruguiera sexangula stand*	279.03	22.10	21.70			Kusmana et al. (1992)
Indonesia (East Sumatra)	103.802865	0.018566	1	Fringe		*Rhizophora apiculata stand*	40.70	2.50	29.50			Kusmana et al. (1992)
Brazil (Bertioga, São Paulo)	-46.206289	-23.897031	2	Fringe		*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	42.30	12.90	6.55	8.72	2160	Lamparelli (1995)
Brazil (Bertioga, São Paulo)	-46.145175	-23.816517	2	Fringe		*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	59.70	16.90	6.83	11.16	1730	Lamparelli (1995)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha^{-1})	BA (m^2 ha^{-1})	H (m)	QSD (cm)	D (st ha^{-1})	Reference
Kenya (Gazi Bay)	39.526721	-4.414226	2	Fringe	14-years-old plantation	*Rhizophora mucronata*	131.60	15.69	8.37	6.24	5132	Lang'at (2008)
Kenya Ramisi estuary)	39.436147	-4.571147	2	Fringe	14-years-old plantation	*Bruguiera gymnorrhiza*	16.65	4.68	4.69	3.60	4600	Lang'at (2008)
China (Dongzhai Bay)	110.618540	19.926986	2		6-years-old plantation	*Sonneratia apetala, Kandelia candel*	38.53	4.83	5.87	9.50	682	Liao et al. (1999)
China (Dongzhai Bay)	110.618540	19.926986	2		6-years-old plantation	*Sonneratia apetala*	20.01	6.03	6.70	9.70	817	Liao et al. (1999)
Panama (Bocas del Toro)	-82.263856	9.352515	7	Fringe		*Rhizophora mangle*	59.50	15.80	3.94	4.87	8500	Lovelock et al. (2005)
Panama (Bocas del Toro)	-82.209274	9.318016	7	Fringe		*Rhizophora mangle*	22.20	11.20	1.54	2.83	17800	Lovelock et al. (2005)
Panama (Bocas del Toro)	-82.086454	9.178210	7	Interior		*Rhizophora mangle*	8.30	6.80	0.74	1.61	33570	Lovelock et al. (2005)
Panama (Bocas del Toro)	-82.247714	9.268186	7	Interior		*Rhizophora mangle*	194.30	30.10	4.14	9.00	4730	Lovelock et al. (2005)
Australia	153.13785	-27.399763	2	Fringe	Mature forest	*Avicennia marina forest*	341.00	38.31	16.40	32.50	462	Mackey (1993)
Australia	153.13785	-27.399763	2	Fringe	Secondary forest 25-years-old	*Avicennia marina forest*	162.00	21.16	9.70	7.42	4900	Mackey (1993)
Australia	153.13785	-27.399763	2	Fringe	Secondary forest 25-years-old	*Avicennia marina forest*	110.00	11.48	5.30	3.88	9700	Mackey (1993)
India (Andaman Island)	92.750000	12.500000	2	Fringe	Primary forest	*Rhizophora apiculata, R. stylosa, R. mucronata*	124.00	5.00	7.50	11.96	445	Mall et al. (1991)
India (Andaman Island)	92.750000	12.500000	2	Interior	Primary forest	*B. gymnorrhiza, B. parviflora, B. cylindrica, C. tagal, L. littorea, A. officinalis, R. mucronata, R. apiculata, S. alba, X. granatum*	214.00	15.70	27.50	14.29	980	Mall et al. (1991)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha⁻¹)	BA (m² ha⁻¹)	H (m)	QSD (cm)	D (st ha⁻¹)	Reference
Brazil (Itamaracá/PE)	-34.850000	-7.800000	2			*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	104.79	14.10	5.20	7.20	3487	Medeiros & Sampaio (2008)
Australia (Kooragang Island)	151.760000	-32.840000	2	Fringe	15-years-old stand	*Avicennia marina*	21.80	9.57	4.40	4.90	5075	Murray (1985)
Australia (Gosford)	151.760000	-32.840000	5	Fringe	15-years-old stand	*Avicennia marina*	21.70	12.49	4.30	4.40	8213	Murray (1985)
Thailand (Trat)	102.571748	12.192538	2	Fringe		*Rhizophora apiculata*	1.91	2.61	1.70	2.74	4440	Okimoto et al. (2013)
Thailand (Southern Pang-nga)	98.520000	8.440000	2		Secondary forest, 15-years-old	*Rhizophora mucronata, Bruguiera cylindrica, Xylocarpus granatum, Sonneratia alba*	62.20	11.40	6.50	7.53	2560	Poungparn et al. (2003); Komiyama et al. (2008)
Thailand (Trat Eastern)	102.520000	12.240000	2		Secondary forest	*Sonneratia caseolaris, avicennia alba, Rhizophora apiculata, Rhizophora mucronata, Bruguiera gymnorrhiza*	142.20	19.00	10.80	12.60	1525	Poungparn et al. (2003); Komiyama et al. (2008)
Brazil (Potengi Estuary)	-35.206947	-5.767478	2	Fringe		*Rhizophora mangle, Avicennia schaueriana, Laguncularia racemosa*	85.96	9.50	5.40	6.20	3200	Ramos-Silva et al. (2007)
China (Leizhou Bay, Guangdong)	110.168069	20.986322	2	Fringe	4-years-old plantation	*Sonneratia apetala*	39.30	9.92	8.40	9.20	1494	Ren et al. (2010)
China (Leizhou Bay, Guangdong)	110.168069	20.986322	2	Fringe	5-years-old plantation	*Sonneratia apetala*	59.60	16.32	10.20	12.00	1444	Ren et al. (2010)
China (Leizhou Bay, Guangdong)	110.168069	20.986322	2	Fringe	8-years-old plantation	*Sonneratia apetala*	76.40	19.42	11.40	13.40	1378	Ren et al. (2010)
China (Leizhou Bay, Guangdong)	110.168069	20.986322	2	Fringe	10-years-old plantation	*Sonneratia apetala*	82.10	20.72	13.30	14.10	1328	Ren et al. (2010)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha^{-1})	BA (m^2 ha^{-1})	H (m)	QSD (cm)	D (st ha^{-1})	Reference
USA (Florida)	-80.270000	25.670000	6	Fringe		*Rhizophora mangle, Laguncularia racemosa, Avicennia germinas*	56.00	13.54	4.00	1.02	165000	Ross et al. (2001)
Dominican Republic	-69.670000	19.170000	2	Fringe/Interior	50-years-old	*Rhizophora mangle, Laguncularia racemosa, Avicennia germinas*	233.00	26.80	24.00	18.33	1016	Sherman et al. (2003)
Brazil (Sepetiba Bay, Rio de janeiro)	-43.590000	-23.020000	3	Fringe		*R. mangle, L. racemosa, Avicennia schaueriana*	65.40	21.60	6.10	7.80	4510	Silva (1988); Silva et al. (1991, 1998)
Brazil (Bertioga, São Paulo)	-46.210000	-23.900000	2	Interior		*Rhizophora mangle, Laguncularia racemosa*	51.54	6.02	7.70	7.50	2560	Soares & Schaeffer-Novelli (2005)
Brazil (Sepetiba Bay, Rio de Janeiro)	-43.590000	-23.020000	3	Fringe/ Interior		*Rhizophora mangle, Laguncularia racemosa*	166.58	12.32	7.63	8.80	4100	Soares & Schaeffer-Novelli (2005)
South Africa	31.035633	-29.807950	3		32-years-old forest	*Bruguiera gymnorrhiza*	74.67	23.61	5.50	2.66	42500	Steinke et al. (1995)
South Africa	31.035633	-29.807950	3		32-years-old forest	*Avicennia marina*	19.82	7.35	5.50	4.56	4500	Steinke et al. (1995)
Indonesia (Java)	109.200000	-7.280000	2	Fringe	7-years-old plantation	*Rhizophora mucronata*	93.73	12.71	5.93	5.91	3270	Sukardjo & Yamada (1992)
Japan (Okinawa)	127.680000	26.190000	3		Primary forest	*Rhizophora mucronata*	108.10	31.00	5.50			Suzuki & Tagawa (1983)
Japan (Okinawa)	127.680000	26.190000	3		Primary forest	*Bruguiera gymnorrhiza*	97.60	32.90	5.50			Suzuki & Tagawa (1983)
Japan (Okinawa)	127.680000	26.190000	3		Primary forest	*Rhizophora mucronata, Bruguiera gymnorrhiza*	78.60	22.70	5.50			Suzuki & Tagawa (1983)
China (Shenzhen)	114.060000	22.540000	2		22-years-old forest	*Aegiceras corniculatum*	68.07	1.29	3.85	19.56	5290	Tam et al. (1995)
China (Shenzhen)	114.060000	22.540000	2		22-years-old forest	*Kandelia candel*	10.58	0.16	4.20	7.76	780	Tam et al. (1995)
China (Shenzhen)	114.060000	22.540000	2		Stunted, 22-years-old forest	*Avicennia marina*	8.49	0.04	4.35	13.63	260	Tam et al. (1995)

Location	LonDD	LatDD	Env. Setting*	EcoType**	Condition	Spp composition	AGB (t ha⁻¹)	BA (m² ha⁻¹)	H (m)	QSD (cm)	D (st ha⁻¹)	Reference
Thailand (Ranong Southern)	98.610000	9.950000	2	Fringe/ interior	Primary forest	*R. apiculate, R. mucronata, B. cylindrica, B. gymnorrhiza, B. parviflora, C. tagal, C. decandra, Derris indica, H. littoralis, S. alba, A. corniculatum, Avicennia alba, A. officinalis*	281.20	23.97	10.64	10.90	1246	Tamai et al. (1986)
Colombia (Rancheria river delta)	-72.892606	11.540390	2	Fringe		*Laguncularia racemosa, Rhizophora mangle*	70.98	13.30	6.10	10.81	1449	Vélez & Polanía (2007)
Colombia (Rancheria river delta)	-72.901367	11.553472	2	Interior		*Avicennia germinas*	26.80	5.50	4.40	6.71	1557	Vélez & Polanía (2007)
China (Yingluo Bay)	109.751300	21.572122	2	Fringe		*Avicennia marina*	40.01	75.88	1.44	4.10	57500	Wang et al. (2013)
China (Yingluo Bay)	109.753611	21.564475	2	Fringe		*Sonneratia apetala*	153.23	36.33	3.25	2.13	102000	Wang et al. (2013)
China (Yingluo Bay)	109.764239	21.569153	2	Interior		*Aegiceras corniculatum, Kandelia obovata*	97.17	128.06	2.40	4.77	71700	Wang et al. (2013)
China (Yingluo Bay)	109.767556	21.554500	2	Interior		*Bruguiera gymnorrhiza*	148.71	139.77	2.43	4.79	77600	Wang et al. (2013)
China (Yingluo Bay)	109.775300	21.536556	2	Interior		*Rhizophora stylosa*	270.59	76.29	3.35	7.41	17700	Wang et al. (2013)

* Environmental settings after from Thom (1982) and Woodroffe (1992). Environmental settings # 1-7 denote, respectively, deltaic, estuarine, lagoon, composite, bedrock valley, low carbonate island, and high island.
** After Schaeffer-Novelli et al. (2000, 2005).

Appendix S1 References List

See Appendix 1 – Data Sources in the main text for the complete list of references cited in this appendix.

Supporting Information – Appendix S2
Rovai et al. - Scaling mangrove aboveground biomass from site-level to continental-scale

APPENDIX S2

Methods - References used in the mangrove AGB continental-scale modeling analyses

The main objectives of our literature review were to retrieve all studies reporting mangrove forest structure and aboveground biomass (AGB) in the Neotropics and compile a database for this biogeographic region. This dataset includes published (peer-reviewed articles, books, book chapters) and unpublished studies (graduate thesis and dissertations, institutional reports). A literature search was performed primarily online (Scopus, ISI, Biological Abstracts, Scielo, BDTD Database, CAPES Thesis Database, and Google Scholar) using broad search terms such as "mangrove" plus "aboveground biomass", "AGB", "carbon", "productivity", "wood production", "forest structure", "QSD" (quadratic mean diameter), "DBH" (diameter at breast height), and "D130" (diameter measured at 130 cm from the ground). A number of searches were performed in English, Spanish and Portuguese languages. The key words were also linked to country names where mangrove forests are present in the Neotropics. Once an article was retrieved, we also reviewed the document list of references to complement the online search. Since Brazil has the largest mangrove extension in the Neotropics (962,683 ha, Giri et al., 2011) and occupies the third place globally, we also reviewed potential non-published information listed in curriculums of mangrove researches using the Lattes researchers database (Lane, 2010).

Appendix S2 list of references

See Appendix 1 – Data Sources in the main text for the complete list of references cited in this appendix and used in the mangrove AGB continental-scale modeling analyses.

Supporting Information – Appendix S3
Rovai et al. - Scaling mangrove aboveground biomass from site-level to continental-scale

APPENDIX S3

Methods - Variables used to develop a continental-scale mangrove AGB model

A. Information Sources

Climate variables were retrieved from the WorldClim database (period: 1950 -2000) (Hijmans et al., 2005). These variables include minimum temperature of the coldest month (Tmin, °C) and precipitation of the driest month (Pmin, mm yr^{-1}). We used minimum values for both of these variables, rather than mean winter temperature (i.e., mean temperature of the coldest quarter), or seasonal accumulated precipitation (i.e., precipitation of the coldest quarter). The selection of variables was based on the assumption that plants are adapted to cope with climate variability by shifting biomass allocation patterns that are triggered by ecophysiological thresholds (Cavanaugh et al., 2014; Chapman, 1975; Easterling et al., 2000; Lugo & Patterson, 1977; Soares et al., 2012). The minimum temperature of the coldest month and the precipitation of the driest month represent extreme or limiting environmental factors. In contrast, the mean temperature of the coldest quarter and the precipitation of the driest quarter represent the mean winter temperature and the total precipitation, respectively. Since these variables are estimated over a period of three consecutive months, the mean values might no necessarily represent ecophysiological thresholds.

Average annual potential evapotranspiration (PET, mm yr^{-1}) was calculated for the period 2000 to 2012 using data from the Moderate Resolution Imaging Spectroradiometer (MODIS) that globally covers vegetated land surface area at a 8-day interval (Chen et al., 2002; Mu et al., 2011a).

Growing degree-days (GDD), an index that describes the heat energy received by a given unit of area over a given time period, was computed from the equation

$$GDD = \left(\frac{T\max + T\min}{2} \right) - Tbase$$

(1)

where Tmax is the maximum and Tmin the minimum air temperatures; Tbase is the mean temperature of the coldest month (McMaster & Wilhelm, 1997). GDD was calculated using WorldClim variables (Hijmans et al., 2005) based on the latitudinal temperature range where mangrove wetlands occur (Giri et al., 2011).

A global tidal range was calculated using the tidal atlas of finite element solutions (Carrère et al., 2012) by subtracting mean low water springs (MLWS) from mean high water springs (MHWS) (≈ MHWS - MLWS). The highest value of the sum of the two major tidal constituents, either the semidiurnal amplitude (M2 + S2) or diurnal amplitude (K1 + O1), was used for each grid cell where mangrove aboveground biomass was estimated; these values were then multiplied by two to obtain the tidal range (TR, cm).

The global river discharge data (RD, m^3 s^{-1}) was extracted from the Global Runoff Data Centre - GRDC (Fekete et al., 2002).

B. Evaluation criteria used in the auto-correlation, multicollinearity tests, and automated model selection analyses

1) Auto-correlation, multicollinearity tests

All pre-selected variables to be included in the continental scale-model were tested for autocorrelation (Spearman's rank) and multicollinearity (variance inflation factor – VIF). The thresholds used to include variables in the regression analyses were: $r^2 < 0.5$ and VIF < 10 (for details see Dormann et al., 2013).

2) Automated model selection analyses

First, we applied a multi-model inference approach based on Akaike's information criterion – AIC (Akaike, 1974), which generates a set of models with different combinations of variables to be included in the continental-scale mangrove AGB model. Only models with a criterion of $\Delta AIC < 7$ were considered further since fitted models with values above this threshold fail to substantially explain data variability (Burnham & Anderson, 2002). Then, the significance ($\alpha < 0.05$) of the terms for each selected model was assessed coupling OLS summary outputs, ANOVA, and a stepwise (backward and forward) model selection. The R-anova function evaluates whether the model variables in a linear model class-object are statistically significant (R Core Team,

2013). The relative importance of each variable in the model was determined based on R^2 partition where the inclusion level was held at $\geq$ 5%.

List of references cited in this appendix

See Appendix 1 – Data Sources in the main text for the complete list of references cited in this appendix.

Supporting Information – Appendix S4
Rovai et al. - Scaling mangrove aboveground biomass from site-level to continental-scale

APPENDIX S4

Methods - Statistical routines and R packages algorithms

1) Null model probability analysis
- Empirical Cumulative Distribution Function - stats (R Core Team, 2013)

2) Multicollinearity
- Autocorrelation (Spearman's rank) - corrgram (Wright, 2013)
- Variance Inflation Factor (VIF) - usdm (Naimi, 2014)

3) Multiple regression (OLS)
- Linear model - stats (R Core Team, 2013)

4) Model evaluation procedures
- Multi-model inference approach based on Akaike's information criterion (AIC) - muMIn (Bartón, 2004)
- OLS summary outputs - stats (R Core Team, 2013)
- anova - stats (in this package, R-anova function evaluates whether the model variables in a linear model class-object are statistically significant; R Core Team, 2013).
- Stepwise (backward and forward) model selection - MASS (Venables & Ripley, 2002; Ripley et al., 2014)
- Relative importance based on R^2 partition - relaimpo (Groemping, 2006)

5) Lack of fit
- Pure error analysis - alr3 (Weisberg, 2005, 2011).

6) Pairwise tests
- Pairwise Wilcoxon rank sum tests - stats (R Core Team, 2013)

7) Rasters manipulation, and AGB predictions
- raster (Hijmans, 2013)
- rgdal (Bivand et al., 2013)

List of references cited in this appendix

See Appendix 1 – Data Sources in the main text for the complete list of references cited in this appendix.

Supporting Information – Appendix S5
Rovai et al. - Scaling mangrove aboveground biomass from site-level to continental-scale

APPENDIX S5

Results - Regression parameters of the models evaluated

Table S5-1. Model regression parameters evaluated using automated multi-model inference analyses and OLS summary outputs. Small caps letters indicate statistical significance ($\alpha<0.05$) based on the model selection method: a-OLS summary outputs; b-anova function in R; c-stepwise model selection. Boldface indicates the model parameters included in the model used in the prediction analysis.

MODEL (Global) #	Int.	Pmin	Tmin	PET	RD	TR	Pmin: Tmin	Pmin: PET	Tmin: PET	Pmin: Tmin: PET	R^2	Adj. R^2	F value	P value	df	AIC	ΔAIC
1	11.89	-0.247	-0.201	-0.003	0.006	0.001	0.011	1.099e-04	6.16e-02	-4.592e-06	0.25	0.19	4.36	6.535e-05	9		
2	**9.026**	**-0.064**	**-0.067**	**-0.002**		**0.001**	**0.002**	**1.365e-05**			**0.23**	**0.19**	**5.88**	**2.129e-05**	**8**	**319.48**	**0.00**
		(a)	(b)	(a, b)		(a, c)	(a, b, c)	(a, b, c)									
3	8.962	-0.064	-0.075	-0.002	0.007	0.001	0.002	1.397e-05			0.24	0.19	5.20	3.418e-05	9	320.61	1.13
		(a)	(a, b)	(a, b)		(a, c)	(a, b, c)	(a, b, c)									
4	11.454	-0.250	-0.169	-0.003		0.001	0.011	1.119e-04	4.975e-05	-4.698e-06	0.25	0.20	4.79	4.091e-05	10	321.16	1.68
		(a)	(b)	(b)		(a, c)	(b)	(b)		(c)							
5	6.764	-0.061	0.049	-0.001		0.001	0.002	1.371e-05	-5.369e-05		0.23	0.18	5.03	5.119e-05	9	321.60	2.12
		(a)	(b)	(b)		(a, c)	(a, b, c)	(a, b, c)									
6	8.373	-0.058	-0.038	-0.002			0.002	1.181e-05			0.20	0.16	5.88	6.831e-05	7	322.32	2.84
		(a)	(b)	(a, b)			(a, b, c)	(a, b, c)									

MODEL #	Int.	Pmin	Tmin	PET	RD	TR	Pmin: Tmin	Pmin: PET	Tmin: PET	Pmin: Tmin: PET	R^2	Adj. R^2	F value	P value	df	AIC	ΔAIC
7	11.886	-0.247	-0.202	-0.003	0.006	0.001	0.011	1.099e-04	6.155e-05	-4.592e-06	0.25	0.19	4.36	6.535e-05	11	322.58	3.10
		(a)	(b)	(a, b)		(c)	(b)	(b)		(c)							
8	7.337	-0.062	0.009	-0.001	0.006	0.001	0.002	1.399e-05	-3.864e-05		0.24	0.18	4.53	8.013e-05	10	322.86	3.38
		(a)	(b)	(b)		(a, c)	(a, b, c)	(a, b, c)									
9	8.303	-0.058	-0.044	-0.001	0.006		0.002	1.206e-05			0.20	0.16	5.04	0.000122	8	323.66	4.17
		(a)	(b)	(a, b)			(a, b, c)	(a, b, c)									
10	10.867	-0.250	-0.143	-0.003			0.011	1.127e-04	5.087e-05	-4.821e-06	0.22	0.17	4.64	0.000128	9	323.88	4.40
		(a)	(b)	(b)			(b)	(b)		(c)							
11	6.045	-0.055	0.081	0.000			0.002	1.187e-05	-5.529e-05		0.20	0.16	4.90	0.000165	8	324.39	4.91
		(a)	(b)	(b)			(a, b, c)	(a, b, c)									
12	11.243	-0.247	-0.171	-0.003	0.005		0.011	1.109e-04	6.144e-05	-4.728e-06	0.22	0.17	4.14	0.000222	10	325.48	6.00
		(a)	(b)	(b)			(b)	(b)		(c)							
13	6.547	-0.056	0.046	-0.001	0.006		0.002	1.209e-05	-4.177e-05		0.20	0.16	4.30	0.000283	9	325.86	6.38
		(a)	(b)	(b)			(a, b, c)	(a, b, c)									

Results – Fitted model (# 2, Table S5-1) residual analyses

Figure S5-1. Residues analyses of selected model (model # 2, Table S5-1**)** used to predict mangrove aboveground biomass in the Neotropics.

Supporting Information – Appendix S6
Rovai et al. - Scaling mangrove aboveground biomass from site-level to continental-scale

APPENDIX S6

Results - Larger, higher definition maps used in figure 3(a-d)
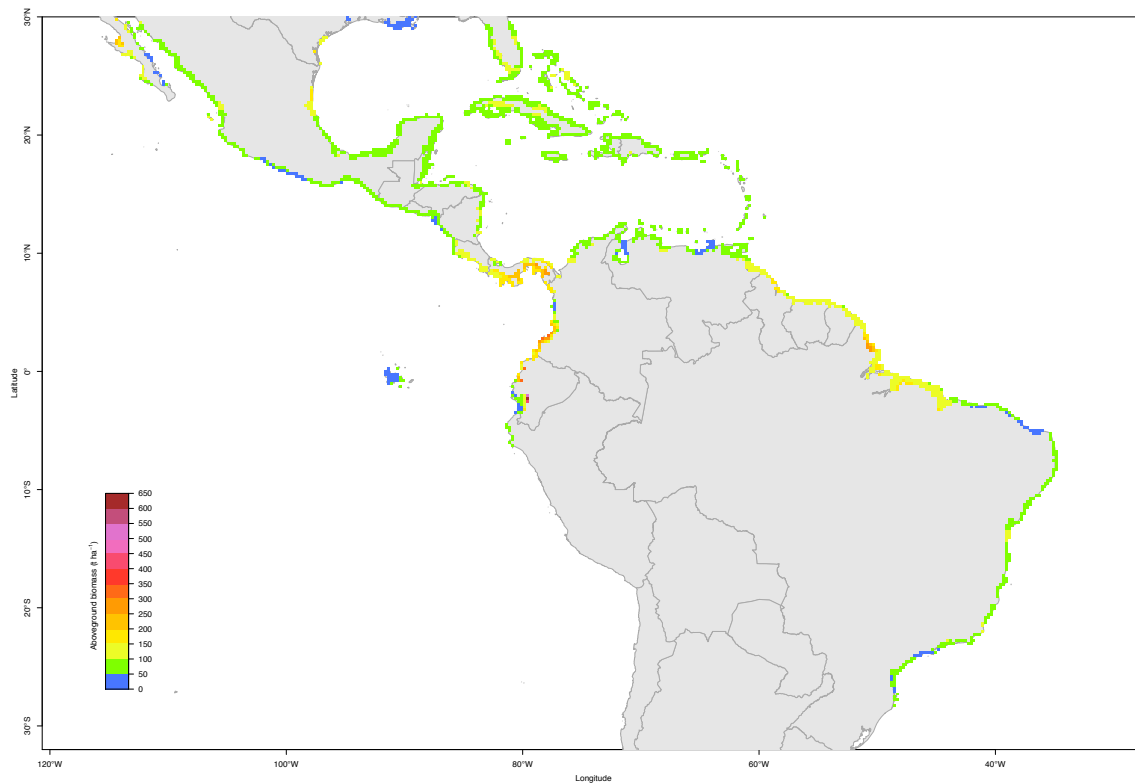
Figure S6−1. Estimated mangrove aboveground biomass (AGB, t ha^{-1}) in the Neotropics using a geophysical−climatic model (also depicted in Fig. 3a). See text for model description and equation.

Figure S6–2. Estimated mangrove aboveground biomass (AGB, ha⁻¹) in the Neotropics using Hutchison et al. (2014) climate–based model (also depicted in Fig. 3b).

Figure S6–3. Estimated mangrove aboveground biomass (AGB, ha^{-1}) in the Neotropics using Saenger & Snedaker (1993) latitude–based model (also depicted in Fig. 3c).

Figure S6–4. Estimated mangrove aboveground biomass (AGB, t ha^{-1}) in the Neotropics using Twilley et al. (1992) latitude–based model (also depicted in Fig. 3d).

3 ECOGEOMORPHOLOGY DRIVES LATITUDINAL VARIATION IN MANGROVE SOIL PROPERTIES[2]
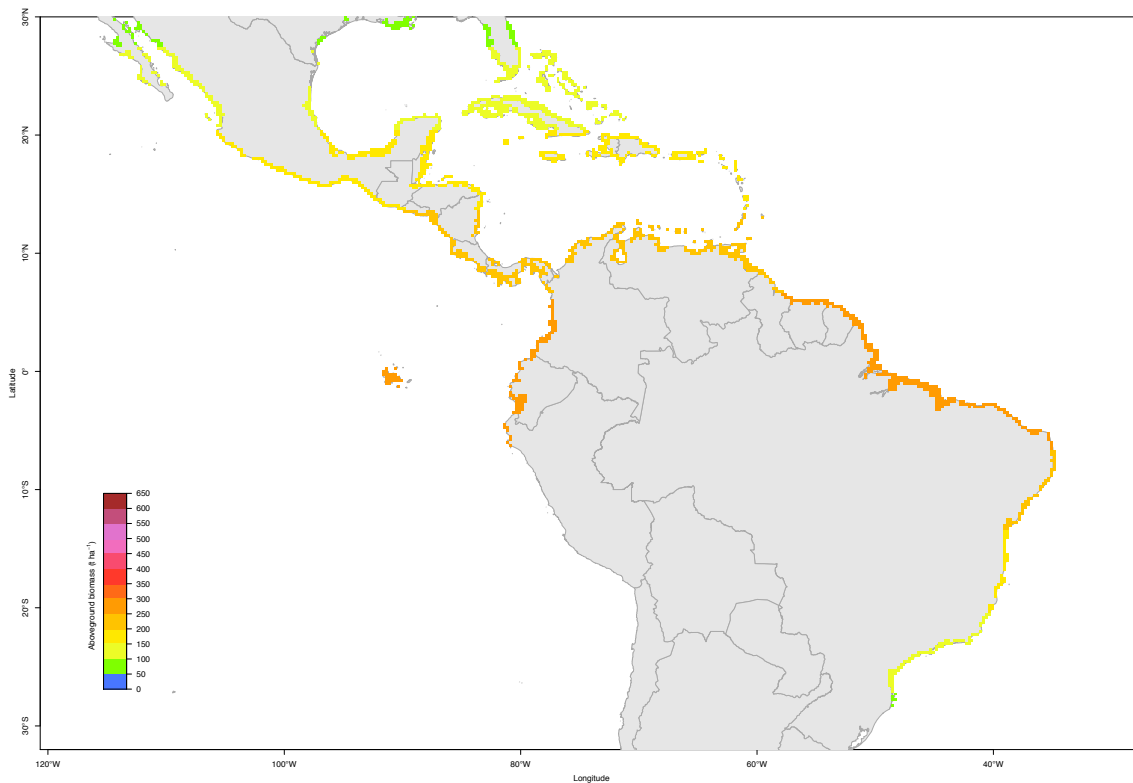
Ecogeomorphogy is an emerging field, which attempts to elucidate questions related to the interface between some combination of hydrology, geomorphology and ecology; that is, it addresses bidirectional influences of biota and landscapes on each other. Nearly fifty years ago, Bruce Thom proposed a conceptual framework based on ecogeomorphology to explain the apparent "chaotic mess of special cases" reported in early mangrove ecological studies. His approach was to classify ecological characteristics of mangroves linked to different coastal environmental settings (CES) based on the repetition of geomorphological processes and landforms. These ideas became the conceptual basis for multiple-scale ecological models to explain global variation in ecosystem properties of mangroves. Here we assessed the concentration and stoichiometry of carbon (C), nitrogen (N) and phosphorus (P) in mangrove soils from 27 sites across the neotropics, including distinct types of CES replicated along a hemispheric range spanning from ~ 29.5° N to 27.5° S. To our knowledge, we provided the first empirical account on the nature of distinct CES properties as related to their ecosystem correlates. Our results showed that ecogeomorphology, rather than latitude gradient-related hypotheses, drives latitudinal variation in mangrove soil nutrient availability and resultant soil C stocks. We suggest that incorporating ecogeomorphic-related forcings (e.g. river discharge, tides) into predictive models is paramount to advance hypotheses and improve our understanding regarding biogeochemical interactions at the land-ocean interface as well as our capacity to foresee the effects of global change on these ecosystems.

The value of coastal wetlands such as mangroves to society is undisputed, particularly when considering their role in exporting significant amounts of C in the form of detritus to estuarine and near coast seabeds, supporting productive fisheries around the world[1]. More recently these ecosystems have been characterized as important in climate change mitigation[2] given mangroves influence coastal carbon

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cycles by storing atmospheric carbon dioxide (CO_2) in its soils where it remains immobile for millennia[3]. Mangrove wetlands play a major role in the global C cycle[4] storing on average five times more C in its soils than other tropical, temperate and boreal terrestrial and aquatic ecosystems, on a per-unit-area basis[5,6]. Because the C-N-P interaction may enhance or weaken the carbon-climate feedback[7,8] reconciling site-specific mechanisms underlying the C:N:P atomic stoichiometric ratios of mangrove ecosystems to large-scale global estimates of C stocks is key to advancing hypotheses and improving predictive models to explain the latitudinal variation of C sinks in these and other coastal wetlands. The environmental signature hypothesis (ESH) for tropical coastal ecosystems states that geophysical forcings, along with regional climate, control the latitudinal variation in soil biogeochemistry, ultimately determining C partition and nutrient conservation stragies within these systems[9,10]. We propose that the ESH is viable method to explain such large-scale variation in soil inventories that can improve estimates of global sinks along continental margins. Although it is not the realm of this study to review large-scale hypotheses-testing investigations in mangroves, to our knowledge mangrove macroecology remains as an emergent science, with only a handful of studies addressing ecological trends at that scale[4,11,12]. In addition, the broad distribution along the world's tropical and subtropical shorelines[13] and over a variety of costal environmental settings (CES), from deltaic to karstic landforms[14], enable such investigations. In addition, a well defined evolutionary trait, and low variation in habitat complexity, make mangroves a good ecological group to use for macroecological investigations[12].

3.1 BOTTLENECKS IN MANGROVE SOIL MACROECOLOGY

Attempts to explain much of the large-scale patterns of nutrient storages and C allocation strategies in mangrove forests have been grounded on ecological theory developed for upland forests. For instance, the geochemical hypothesis, which states that tropical soils from upland forests are more weathered and thus have lower P availability, has been proposed to explain latitudinal variation in mangrove soil P limitation[11]. Soil P limitation is tightly related to mangrove C allocation strategies, as demonstrated by comparing mangroves in karstic environments[15]. In addition, the combination between geographical sampling bias (e.g., scarce and uneven distributed sampling points) and the choice of environmental predictors used in contemporary global mangrove soil C assessments[16], have been

hindering the development of models capable of delivering more precise soil global C estimates. Other approaches to global soil C assessments is the use of apparent direct aboveground-belowground biomass allometric relationships to estimate global soil C storage[17]. While these models may provide a first glance at the spatial distribution and magnitude of soil C stocks, they overlook nutrient allocation patterns [18,19] explained by ecogeomorphology[9,10] theories, and do not fully address important drivers of mangrove soil stoichiometry and its influence for ecosystem C allocation strategies. In mangrove wetlands, it is assumed that the combination of hydrology and climate (i.e., environmental signature) control soil biogeochemistry[10]. Collectively, these environmental forcings determine the load and the concentration of P (e.g., N:P stoichiometric ratio) at any given CES, which in turn reflects the partitioning of C between below- and aboveground ecosystem compartments[20].

3.2 LATITUDINAL VS. REGIONAL CONTROLS OF MANGROVES SOIL BIOGEOCHEMISTRY

Our experimental approach was to assess the significance of key environmental drivers to the formation of conspicuous CES, and to test the influence of these coastal settings in determining mangrove soil biogeochemistry. To test our assumptions we replicated and varied distinct CES with latitude. We determined the concentration and stoichiometry of C, N and P in mangrove soils from 27 sites across the neotropics, selected across distinct types of CES replicated along an hemispheric range spanning from ~ 29.5°N to 27.5°S (Fig. 1). Here we show that ecogeomorphology using the ESH, rather than latitude gradient-related hypotheses, drives latitudinal variation in mangrove soil C stocks and C:N:P stoichiometry, and discuss the implications of our findings for contemporaneous global soil C estimates. We also predicted that regional factors, including geophysical forcings (river discharge, tidal amplitude), along with regional climate (temperature, precipitation, and evapotranspiration) shape conspicuous CES, which ultimately determines mangrove soil N an P concentrations and stoichiometry, and resulting soil C stocks.

Mangrove soil C and total N concentrations (g cm^{-3}) increased with latitude (R^2=0.19 and 0.27, respectively, df=79; p<0.05 for this and following analyses) (Fig. 2) and were consistent with hypotheses of terrestrial forests (i.e. high soil density in high latitude, and low soil density in low latitudes)[21]. This pattern adheres to the metabolic theory for terrestrial vegetation, where organic matter decay rates slow down

polewards[22,23]. With regards to the latitudinal variation in mangrove soil P limitation we confirmed our hypothesis that the concentration of P is not correlated with latitude (R^2=-0.01, p=0.52). Following the trends observed for C and N, the atomic ratios N:P and C:P of mangrove soils increased with latitude (R^2=0.19 and 0.10), while C:N ratios slightly decreased with latitude (R^2=0.05). However, despite apparent trends with latitude, the dispersion of data-points in the regressions suggests the influence of CES in determining mangrove soil properties. A closer look at the variance components (VC) of the two-way ANOVA (factors "CES" and "site") revealed that much of the variability regarding the nutrient concentration and stoichiometry of mangrove soils was in fact due to the type of CES (Fig. 3). VC values for the factor CES ranged from 42% for P to 64% for N, while sites explained to a lesser extent the variability among factors (16% for N, and 40% for P). With regards to the C:N:P stoichiometry across CES, coastal landscapes with river discharge had low, narrow ratios (282:09:1 to 662:20:1) while karstic and landforms with no river discharge had high, wide ratios (760:39:1 to 2923:117:1) due to high soil C density and limited P concentration (Supplementary Table S1). In addition, the resulting differentiation between CES (post-hoc tests) indicated the formation of groups with similar soil N and P concentration and stoichiometric ratios (Supplementary Fig. S1). The cohesion of such groups was further scrutinized using multivariate analyses (Fig. 4; see methods for details). Differences among CES were significant, except for tide- and wave-dominated deltaic, and carbonate and composite (wave/river-dominated). In addition, the following environmental correlates explained the gradient formed in the ordination analysis: temperature of the coldest month (Tmin, °C), precipitation of the driest month (Pmin, mm yr^{-1}), potential evapotranspiration (PET, mm yr^{-1}), tidal range (TR, cm), and river discharge (RD, $m^3 s^{-1}$). The gradient spanned from sites that receive river input and have low N:P ratios (tide- and wave-dominated deltaic settings) to P-limited sites with negligible or no river input (carbonate and composite CES).

3.3 TRANSITION TO AN ECOGEOMORPHOLOGICAL APPROACH

Whilst foliar N and P concentrations have been largely used as a proxy to explain global soil nutrient limitation, within tropical forests these oversimplifications mask critical variation in the extent and nature of nutrient limitation at multiple scales[24]. A potential confounding factor

in foliar N:P latitudinal trends is the paucity of data; much of the studies developed for upland biomes lack substantial information on tropical forests[22,23,25], and mangrove forests are virtually absent in these analyses. Further, when constrained to the tropics, the main latitude-based variables (e.g. mean annual temperature and precipitation) did not explain the hemispheric variability in leaf N:P resorption efficiency ratios[22]. Thus, considering tropical forests are arguably the most biogeochemically diverse biome on the planet, the use of N:P ratios (e.g. foliar, microbial biomass) to infer larger-scale ecosystem processes should be exercised with caution, and such attempts must comprehensively account for the diversity of any given site and recognize the broad range in nutrient requirements[21,24]. Remarkably, the environmental diversity of mangrove forests surpasses that of their tropical terrestrial counterparts; unlike upland vegetation, these forested wetlands are subjected to circadian flooding by tides, occupying mostly waterlogged saline soils with high levels of sulfides[20]. Environmental gradients imposed by the distance along estuarine longitudinal and subtle changes in the topography (at the millimeter scale in elevation) perpendicular to water bodies originate new sets of variables to be factored in, which will collectively reflect on nutrient conservation strategies (i.e., plant-soil interactions).

Here, we provided the first empirical account on the nature of distinct CES and their environmental correlates in support of the ESH for mangroves[9,10,14]. The ESH for tropical coastal ecosystems states that geophysical forces (river discharge, tides), along with regional climate (temperature, precipitation, PET), control soil biogeochemistry, ultimately determining the structure (e.g., basal area, tree height) and function (e.g., net primary productivity - NPP) of these ecosystems[10]. Not only is this most important and readily applicable to other flood pulse-dominated systems, given large similarities in structural and functional traits across freshwater and salt-water environments[26], but it also underscores that adopting geomorphic-related forcings (e.g. river discharge, tides) into predictive models is paramount. Currently, we lack such models[16], and arguably they would advance our ecological understanding regarding the spatial distribution and the magnitude of nutrient availability, which in turn is tightly coupled to ecosystem-level C allocation strategies. Biomass (or C) partitioning in mangroves responds to complex interactions between resources (nutrients, light, space), regulators (salinity, sulfide, pH, redox) and hydroperiod[20]. These drivers vary in magnitude across local to regional scales[27], as observed in relatively short stretches of shoreline with heterogeneous coastal

landforms (i.e., deltaic, embayments, and composite landscapes). This variation in CES causes much of the variability in edaphic conditions, and thus in structural and functional attributes of mangroves, at any particular latitude[4]. This implies the prevalence of regional rather than climatic controls where, along with weather and relative sea-level change, soil properties and therefore structural and functional diversity of mangroves are constrained by geomorphological boundaries[14]. Most inferences on large-scale ecological trends (e.g. macroecological investigations) in mangrove forests have been made on the basis of leaf traits, with relatively shortage of data on other ecosystem properties. Though this does not represent a fault on the part of the authors but rather scantiness of data, inferences on larger-scale ecosystem processes may be compromised when scaling up solely from physiological responses[24]. For instance, while some physiological traits (e.g. at the leaf level) in mangrove vegetation are readily apparent and straightforward to interpret in light of latitudinal variation[12], only about 20% of the hemispheric variation in aboveground biomass is explained by latitude-related forcings. It is believed that the unaccounted variability is likely due to the omission of key regional and local drivers[28]. To our knowledge, the only attempt to explain latitudinal variability in mangrove soil nutrient limitation has been limited to and inferred from leaf-level ecophysiological traits[11]. In this analysis, nutrient conservation mechanisms at the leaf level (phosphorus resorption efficiency during leaf senescence), rather than direct soil fertility tests, were used to suggest the presence in the vegetation of a geochemical signature that supposedly has evolved in response to historically low P availability in the tropics[11]. Our findings, however, diverge from this latitude-based framework proposed to account for the spatial variation of P availability in mangrove soils. Instead, regional drivers indicated at the geomorphologic unit level may be constraining latitudinal variation in both concentration and stoichiometry of soil elements. Particularly, soil P limitation (high N:P ratios) seemed to have been influenced by carbonate (Shark River and Taylor Slough, FL, USA) and composite wave-dominated (Laguna Gandoca, CR) CES, both of which receive, if any, insignificant river input (see Supplementary Table S2 for details on sampling sites). Further, the soil N:P ratios observed across our study sites corroborate the patterns of riverine export of dissolved inorganic phosphorus to the coastal zone[29], with low soil N:P sites (Amazon and Caravelas river deltas) located in the low tropics where most of the major rivers are located[30]. Additionally, low mangrove soil N:P ratios associated with deltaic CES have been registered in temperate river-

dominated coastal landforms[31] as a response to the high yield of rich P-adsorbed sediment particles to coastal waters[29]. Moreover, our results are consistent with a recent global analysis of soil P concentrations in terrestrial ecosystems where insignificant correlations between soil total P and climate variables were found[21]. With regards to the diversity of CES, the C:N:P stoichiometric ratio for mangrove soils (global average 902:38:1) is consistent with ratios described for other natural wetlands (1347:72:1)[21], suggesting a Redfield-type ratio[32] inherent to wetlands. In addition, our results showed that karstic and alluvial coastal landforms further differentiate into two distinct CES groups, one characterized by low and narrow C:N:P stoichiometric ratios due to the marked contribution of river discharge and the other by high and wide ratios owing to the absence of fresh water inputs and consequent rich-P sediment particles (Supplementary Table S1).

Although we see merit and agree that to some extent ecological theory developed in upland forests can help explain many traits in mangroves[12] we also believe that a more complete understanding of tropical forest ecology, including mangrove forests, across multiple scales still presents one of the grand challenges for ecologists in the coming century[24]. Essentially, there are no universal solutions in ecology and oversimplifications seeking global generality must be viewed with caution[33]. We sustain that mangrove ecology should lead to advances in the fields of both terrestrial and coastal wetland ecology, enhancing our understanding regarding land-ocean interactions as well as our capacity to foresee the effects of global change on these ecosystems.

3.4 METHODS

Study area and sampling strategy. We determined the concentrations and stoichiometry of C, N and P in mangrove soils from 27 sites across the netropics (Fig 1.). Our sampling strategy considered both the absolute latitudinal variation (~ 29.5°N to 27.5°S) and the type of CES as factors, with different types of CES replicated along the hemispheric range investigated. CES were replicated by either sampling mangroves situated in independent watersheds or respecting a minimum distance of fifty kilometers between sampling stations, whenever possible (see Supplementary Table S2 for details). At each sampling station we collected three 1-meter deep cores from which we subsampled the depth intervals 5-10, 20-25, 37.5-42.5, 67.5-72.5 cm[6]. Soil samples were oven-dried at 60°C to a constant weight and weighed to estimate soil bulk density (BD, g dry mass per cm^3 of wet soil). Organic C, and total N

were determined via dry combustion using an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California) after acid fumigation to remove carbonates[34]. Total P was extracted with 1 N HCl after combustion in a furnace at 550°C[35] and determined by colorimetric analysis using a Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas). Mean soil nutrient concentrations (g cm^{-3}) up to a depth of 1 meter were computed by averaging the products between nutrient percentage values and BD obtained for each depth interval. The stoichiometry of C, N and P in mangrove soils was calculated on a molar basis.

Climatic and geophysical data compilations. Environmental variables for each grid cell where we sampled mangrove soils were retrieved from a variety of global databases. Climate variables were retrieved from the WorldClim database for the period 1950-2000[36]. These variables include minimum temperature of the coldest month (Tmin, °C) and precipitation of the driest month (Pmin, mm yr^{-1}). The selection of variables was based on the assumption that plants are adapted to cope with climate variability by shifting biomass allocation patterns that are triggered by ecophysiological thresholds[28,37]. The minimum temperature of the coldest month and the precipitation of the driest month represent extreme or limiting environmental factors. Average annual potential evapotranspiration (PET, mm yr^{-1}) was calculated for the period 2000 to 2012 using data from the Moderate Resolution Imaging Spectroradiometer (MODIS) that globally covers vegetated land surface area at a 8-day interval[38,39]. A global tidal range was calculated using the tidal atlas of finite element solutions[40] by subtracting mean low water springs (MLWS) from mean high water springs (MHWS) ($\approx$ MHWS - MLWS). The highest value of the sum of the two major tidal constituents, either the semidiurnal amplitude (M2 + S2) or diurnal amplitude (K1 + O1), was then multiplied by two to obtain the tidal range (TR, cm). The global river discharge data (RD, m^3 s^{-1}) was extracted from the Global Runoff Data Centre - GRDC[41].

Statistical analyses. We used a hierarchical sampling design with the sites nested in CES whereas CES was held as a fixed factor and site as random. Normality and homoscedasticity were checked using Shapiro's and Cochran's tests, respectively, and when necessary data was log transformed (ln(x)+1) to eliminate any major departures from these assumptions. In addition, the impact of non-normal distributions on

analyses outcomes is reduced in nested, balanced sampling designs[42]. The effect of latitude on P availability and limitation, and C:N ratios was verified using linear regression analysis (OLS). Variability in nutrient concentrations and limitation across CES was assessed using one-way analysis of variance (ANOVA) and variance components (VC). The estimation of VC is an important step in ecological ANOVA because it is not constrained by sample size (as are probability-based metrics); rather it provides an estimate of magnitude of effects in ANOVA allowing for the determination of the contribution of a given factor to variability in a response variable[43]. Further, significant differences ($\alpha<0.05$) pointed out in the ANOVA were scrutinized using the Scott-Knott test, a clustering algorithm for multiple comparisons that avoids overlapping, a problem commonly observed in other post-hoc tests (i.e., Tukey, Student-Newman-Keuls), where one or more treatment levels are classified in more than one group[44]. We also performed multivariate ordination analyses to investigate clustering patterns resulting from similarities between the CES studied. Variables to be included in the multivariate ordination analyses were tested for autocorrelation (Spearman's rank) and multicollinearity (variance inflation factor – VIF) (see Supplementary Figure S2). The thresholds used to include variables in the analyses were: $r^2 < 0.5$ and $VIF < 10$[45]. Homoscedasticity of the multivariate data was assessed through a multivariate analogue of Levene's test for homogeneity of variances, based on average distance of group members to the group centroid (dispersions) in multivariate space[46] (see Supplementary Figure S3). Multivariate analyses were run on log transformed data ($\ln(x)+1$). Group differences were evaluated using non-metric multi-dimensional scaling (nMDS)[47] coupled with permutational multivariate analyses of variance (PERMANOVA)[48], on the basis of Bray-Curtis dissimilarity, using 999 permutations. Differences identified in the PERMANOVA were investigated using a posteriori pairwise permutational multivariate t-tests[48]. Moreover, working under the assumptions of the ESH[10], we tested the influence of ecologically relevant climatic (minimum temperature of the coldest month - Tmin, precipitation - Pmin, potential evapotranspiration - PET) and geophysical (tidal amplitude - TD, and river discharge - RD) variables on mangrove soil stoichiometry using correlation analyses. All statistical analyses were carried out on R (see Supplementary Material for details).

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3.6 ACKNOWLEDGEMENTS

3.7 AUTHOR CONTRIBUTIONS

A.S.R. conceived the paper, performed the statistical analyses and wrote the manuscript draft. P.R.P., R.R.T. and E.C.M. contributed to the development of the work in general and helped writing the final version of paper. M.C.J. contributed with the data sets from Central America.

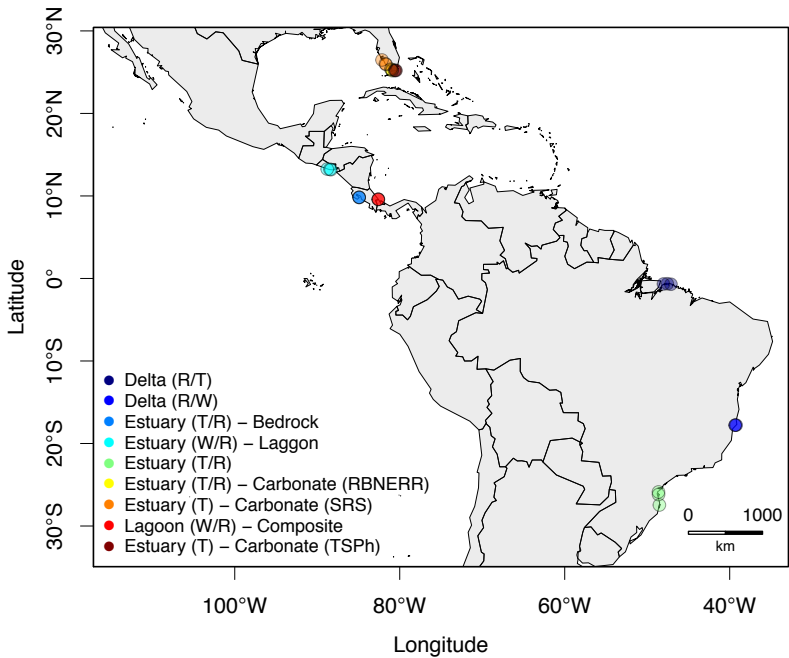**Competing financial interests**

Materials & Correspondence

Figure 1. Sampling points in mangrove wetlands across the Neotropics. The color of the dots (sites) denotes de type of coastal environmental setting (CES) sampled. In each site 3 1-meter deep soil cores were retrieved for the determination of concentrations and stoichiometry of carbon, nitrogen and phosphorus.
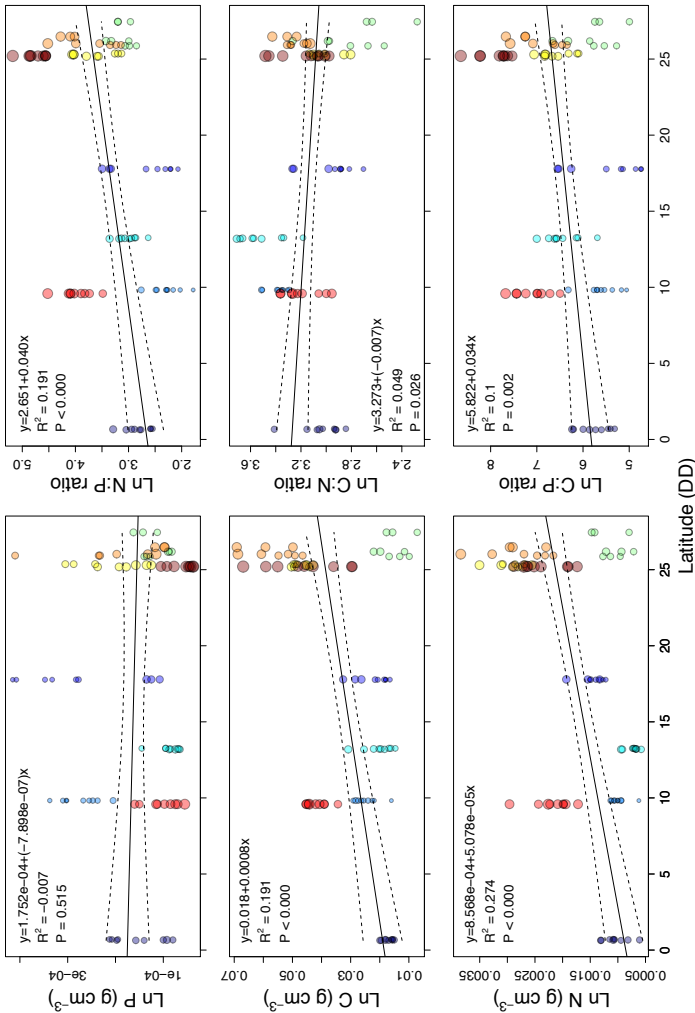
Figure 2. Georelational analyses of soil concentrations and stoichiometry of carbon (C), nitrogen (N) and phosphorus (P), and latitude. Despite the absence of correlation of P with latitude (absolute degrees, in module), or week to moderate relationships observed for C, N, and molar atomic ratios N:P, C:N and C:P, the scatter in the graphs suggests the weight of coastal environmental settings (CES) in determining mangrove soil properties. The colored dots follow the sites and types of CES depicted in figure 1.
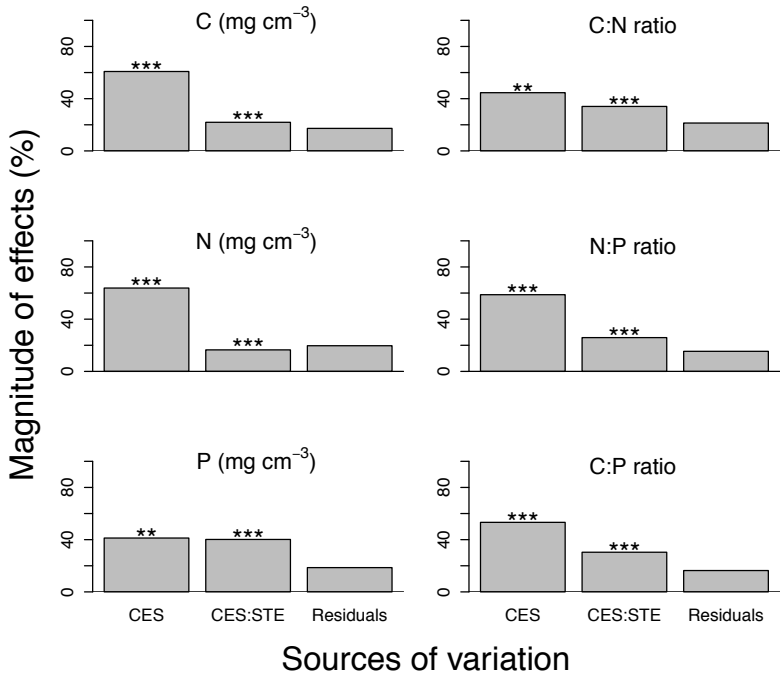
Figure 3. Contribution of factors used in the nested two-way ANOVA to the variability in soil concentrations and stoichiometry of carbon (C), nitrogen (N) and phosphorus (P). The magnitude of effects revealed by the analyses' variance components (VC) indicates the coastal environmental settings (CES), rather than sites (STE, nested effect), explained much of the variability in mangrove soils properties. Asterisks over the bars represent the results of the two-way ANOVA (**<0.01; ***<0.001).
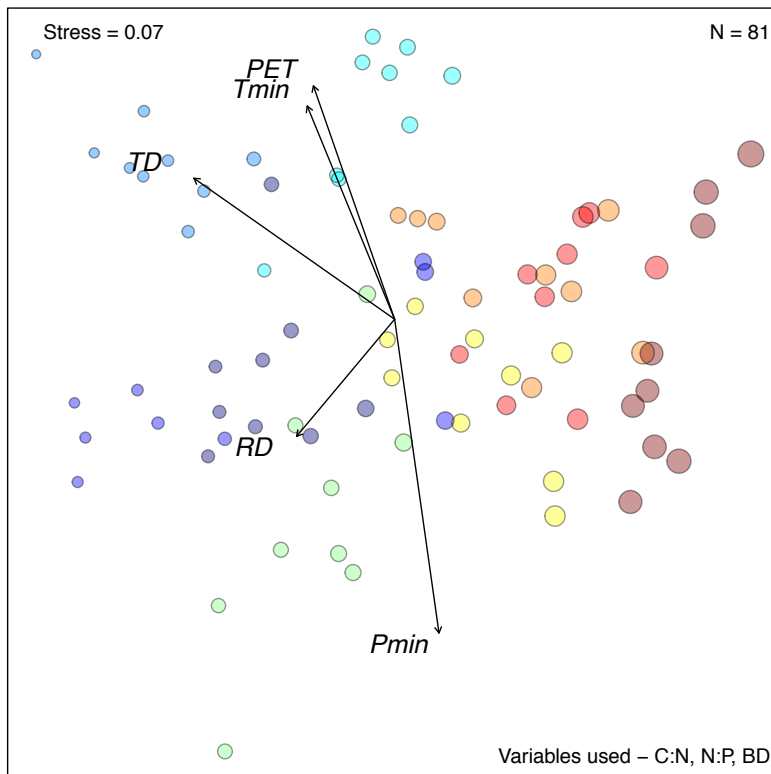
Figure 4. Non-metric multidimensional scaling analysis (nMDS) depicting the grouping of sites into distinct coastal environmental settings (CES), and the environmental correlates (vectors) that explained (α<0.05) the gradient formed in the ordination. The size of the dots is proportional to the N:P ratios observed for each site, spanning from sites that receive river input and have low N:P ratios (tide- and wave-dominated deltaic settings; to the left of the panel) to P-limited sites with negligible or no river input (carbonate and composite CES; to the right). The orientation and length of vectors represent, respectively, the direction and the strength (e.g. correlation between ordination and environmental variable) of the gradient. Tmin - minimum temperature of the coldest month, Pmin - precipitation of the driest month, PET - average annual potential evapotranspiration, TD - tidal range, and RD - river discharge. The colored dots follow the sites and types of CES depicted in figures 1 and 2.

3.8 SUPPLEMENTARY INFORMATION

Supplementary Table S1. Mean concentration of carbon (C), nitrogen (N), phosphorus (P), and C, N and P stoichiometric ratios for mangrove soils for major coastal environmental settings across the Neotropics. Values are presented as means plus standard error (in parentheses). Geomorphological settings classification after Thom (1982)[1].

Coastal Environmental Settings		C (g cm⁻³)	N (g cm⁻³)	P (g cm⁻³)	C:N ratio	N:P ratio	C:P ratio	C:N:P
DT	River delta – Tide-dominated	0.02255 (0.00190)	0.00145 (0.00007)	0.00027 (0.00004)	18.56 (1.32)	15.90 (3.35)	316.36 (82.28)	316:16:1
DT1	River delta – Wave-dominated	0.01734 (0.00061)	0.00104 (0.00008)	0.00015 (0.00002)	20.16 (1.31)	16.36 (1.51)	332.12 (38.47)	332:16:1
BR	Tidal estuary - Bedrock	0.02488 (0.00138)	0.00099 (0.00005)	0.00027 (0.00001)	28.53 (0.80)	09.14 (0.95)	281.58 (38.91)	282:09:1
LG	Tidal estuary – Sand bar lagoon	0.02070 (0.00173)	0.00074 (0.00004)	0.00009 (0.00001)	32.98 (1.95)	19.60 (1.43)	662.08 (79.63)	662:20:1
ET	Tidal estuary	0.01497 (0.00164)	0.00110 (0.00009)	0.00012 (0.00001)	15.40 (1.62)	21.83 (1.47)	354.60 (65.62)	355:22:1
ET2	Tidal estuary – Carbonate setting	0.04828 (0.00096)	0.00292 (0.00010)	0.00021 (0.00002)	19.54 (0.74)	39.04 (4.78)	760.42 (81.49)	760:39:1
ET1	Tidal estuary – Carbonate setting	0.05828 (0.00296)	0.00277 (0.00018)	0.00018 (0.00003)	25.04 (0.82)	48.49 (7.83)	1202.50 (192.02)	1203:48:1
CP	Coastal lagoon – Composite	0.04249 (0.00127)	0.00218 (0.00012)	0.00010 (0.00001)	23.50 (1.20)	54.46 (5.59)	1289.30 (161.48)	1289:54:1
CT	Tidal estuary – Carbonate setting	0.04705 (0.00454)	0.00237 (0.00014)	0.00006 (0.00001)	23.60 (1.65)	116.76 (8.93)	2922.68 (415.71)	2923:117:1
	Global average	0.03295	0.00173	0.00016	23.03	37.95	902.40	902:38:1

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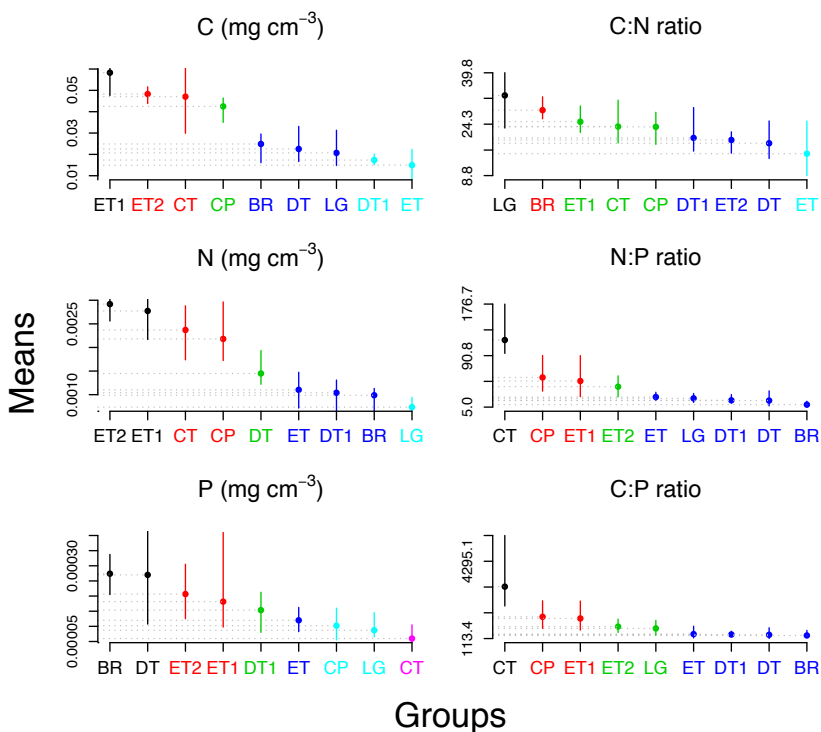
Supplementary Figure S1. Results of the post-hoc multiple comparison test of Scott & Knott (for details see Scott & Knott, 1974; Jelihovschi et al., 2014)[2,3] depicting the differences between types of coastal environmental settings (CES) for carbon (C), nitrogen (N), phosphorus (P) density, and C, N and P stoichiometric ratios for mangrove soils across the Neotropics. Points and vertical lines represent, respectively, the means and the minimum and maximum of the values corresponding to each group mean. The groups are differentiated by colors. The designation of the CES (names in the x axis) follow those described in Supplementary Table S1.

Supplementary Table S2. Description of sampling sites. Geomorphological settings and ecotypes classification after Thom (1982)[1] and Lugo & Snedaker (1974)[4], respectively.

Site ID	Location	Latitude	Longitude	Geomorphological setting	Ecotype
DT-1	Amazon, Pará (Brazil)	-0.667411	-48.031400	River delta – Tide-dominated	Riverine
DT-2	Amazon, Pará (Brazil)	-0.637209	-47.561023	River delta – Tide-dominated	Riverine
DT-3	Amazon, Pará (Brazil)	-0.700967	-47.117270	River delta – Tide-dominated	Riverine
DT1-1	Caravelas, Bahia (Brazil)	-17.769699	-39.332558	River delta – Wave-dominated	Riverine
DT1-2	Caravelas, Bahia (Brazil)	-17.788452	-39.331621	River delta – Wave-dominated	Riverine
DT1-3	Caravelas, Bahia (Brazil)	-17.773427	-39.215733	River delta – Wave-dominated	Riverine
BR-1	Gulf of Nicoya (Costa Rica)	9.824509	-84.914033	Tidal estuary - Bedrock	Fringe
BR-2	Gulf of Nicoya (Costa Rica)	9.826670	-84.917696	Tidal estuary - Bedrock	Fringe
BR-3	Gulf of Nicoya (Costa Rica)	9.827158	-84.920191	Tidal estuary - Bedrock	Fringe
LG-1	Jaltepeque (El Salvador)	13.189806	-88.331444	Tidal estuary – Sand bar lagoon	Fringe
LG-2	Jaltepeque (El Salvador)	13.256417	-88.788167	Tidal estuary – Sand bar lagoon	Fringe
LG-3	Jaltepeque (El Salvador)	13.219111	-88.460333	Tidal estuary – Sand bar lagoon	Fringe
ET-1	Ratones, Santa Catarina (Brazil)	-27.452245	-48.522762	Tidal estuary	Fringe
ET-2	Itapoá, Santa Catarina (Brazil)	-26.183504	-48.623635	Tidal estuary	Fringe
ET-3	Guaratuba, Paraná (Brazil)	-25.870301	-48.630632	Tidal estuary	Fringe
ET2-1	Sanibel, Florida (USA)	26.478160	-82.150279	Tidal estuary – Carbonate setting	Basin
ET2-2	Rookery Bay, Florida (USA)	26.020741	-81.734164	Tidal estuary – Carbonate setting	Basin
ET2-3	Rookery Bay, Florida (USA)	25.927605	-81.652519	Tidal estuary – Carbonate setting	Basin
ET1-1	Shark River-SRS6, Florida (USA)	25.364747	-81.071540	Tidal estuary – Carbonate setting	Fringe
ET1-2	North River, Florida (USA)	25.299336	-80.955321	Tidal estuary – Carbonate setting	Fringe
ET1-3	Coot Bay, Florida (USA)	25.182819	-80.905646	Tidal estuary – Carbonate setting	Fringe
CP-1	Laguna Gandoca (Costa Rica)	9.590426	-82.597870	Coastal lagoon – Composite	Fringe
CP-2	Laguna Gandoca (Costa Rica)	9.588138	-82.597520	Coastal lagoon – Composite	Fringe
CP-3	Laguna Gandoca (Costa Rica)	9.588787	-82.595879	Coastal lagoon – Composite	Fringe
CT-1	Taylor Slough-TSPh7, Florida (USA)	25.204705	-80.642399	Tidal estuary – Carbonate setting	Basin
CT-2	Taylor Slough-TSPh8, Florida (USA)	25.214869	-80.531304	Tidal estuary – Carbonate setting	Basin
CT-3	Taylor Slough, Shell Island, Florida (USA)	25.202916	-80.456374	Tidal estuary – Carbonate setting	Basin
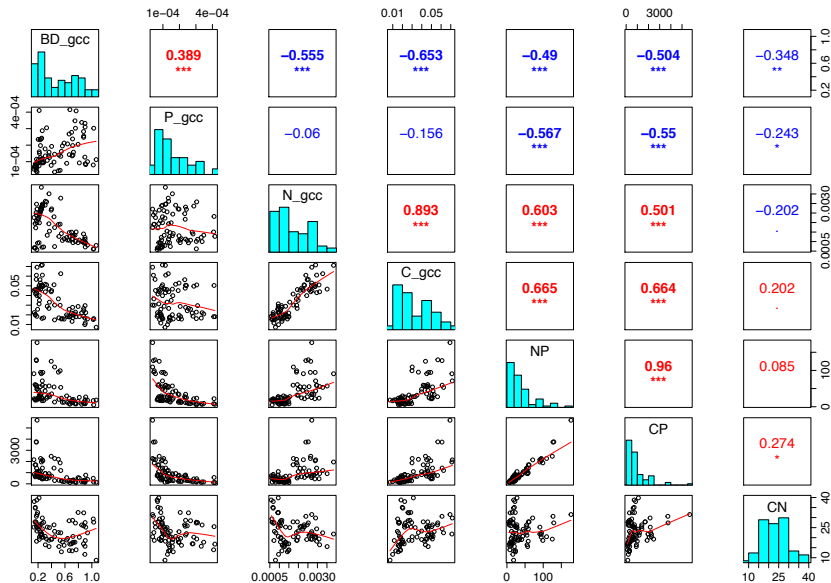
Supplementary Figure S2. Spearman's rank correlation matrix for carbon (C_gcc, in g cm^{-3}), nitrogen (N_gcc) and phosphorus (P_gcc) concentration, bulk density (BD_gcc, in g cm^{-3}), and C, N and P stoichiometric ratios for mangrove soils from major coastal environmental settings across the Neotropics. Histograms display the distribution of the variables. Correlation graphs are shown bellow the histograms while determination coefficients (R^2) and p values (*≤0.05; **≤0.01; ***≤0.001) are presented on the topright half of the panel. Red and blue colors denote, respectively, positive and negative relationships, and bold suggests strong correlation.
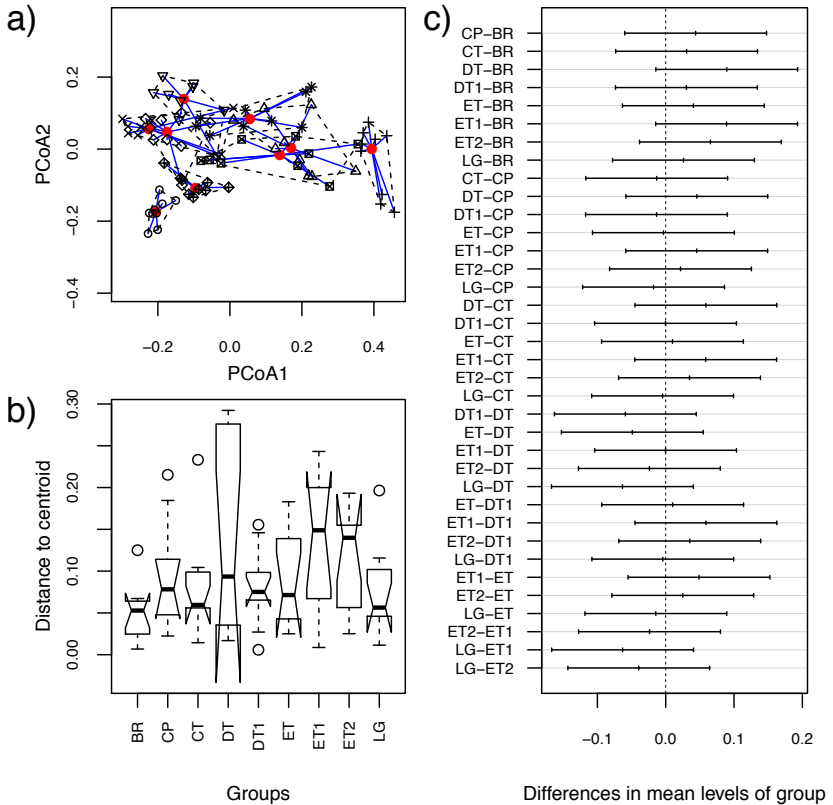
Supplementary Figure S3. A, B - Homoscedasticity of the multivariate data was assessed through a multivariate analogue of Levene's test for homogeneity of variances, based on average distance of group members to the group centroid (dispersions) in multivariate space (for details see Anderson et al., 2006)[5]. C - Assessment of differences between groups using the Tukey's 'Honest Significant Difference' test. Whiskers represent the 95% confidence intervals on the differences between the group means.

R packages and routines used in the statistical analyses

All statistical analyses were carried out on R[6]. Univariate analyses were run using the stats[6] (regression analyses, Shapiro's test) and the GAD[7] (ANOVA, VC, and Cochran's test) packages. Multivariate tests were performed using the vegan[8] (PERMANOVA, nMDS, and correlation analyses) and the RVAideMemoire[9] (distance-based multivariate homogeneity of variance, and post-hoc permutational multivariate t-tests) packages.

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3.9 APÊNDICE – Comprovante de submissão

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4 CONCLUSÃO GERAL

No capitulo 1 deste trabalho foram propostos modelos para estimar a biomassa aérea de manguezais em escalas continentais a partir de dados médios (publicados e não publicados) de estrutura de bosques de mangue. Em comparação com abordagens anteriores, o presente estudo diferencia-se em três aspectos. Primeiro, foi desenvolvido um conjunto de modelos matemáticos que permitem, a partir de dados existentes em escala local (sítio), reciclar e transformar valores médios de estrutura florestal em biomassa aérea e, com estes valores, gerar estimativas mais robustas em macro escala. Segundo, a modelagem realizada neste trabalho inclui variáveis ecologicamente relevantes para variabilidade espacial da biomassa aérea de manguezais, as quais não foram consideradas em estudos pretéritos. Por fim, as estimativas geradas pelos modelos ora propostos foram validadas considerando valores reais de biomassa aérea de manguezais obtidos em campo, oriundos de trabalhos independentes. Vinte porcento da variabilidade latitudinal da biomassa aérea de manguezais na região Neotropical foi explicada pela combinação de fatores geofísicos (amplitude de marés) e climáticos (temperatura, precipitação e evapotranspiração). A fração não explicada pelo modelo foi atribuída a diversidade de ambientes geomorfológicos costeiros presentes na área de estudo. A comparação entre modelos preditivos desenvolvidos para estimar a variabilidade latitudinal dos estoques de C na biomassa aérea de manguezais demonstrou que estimativas globais recentes sobre-estimam entre 25 e 50% a magnitude destas reservas. As implicações desta descoberta repercutem em valores-referência rotineiramente utilizados para determinar os estoques de C e o potencial de emissão de CO_2 resultantes da conversão de áreas de manguezal (SIIKAMÄKI; SANCHIRICO; JARDINE, 2012), bem como em exercícios de valoração ecológico-econômica de serviços ecossistêmicos (COSTANZA et al., 2014). Para o compartimento aéreo, o avanço na área de modelagem global dos estoques de C se deu em virtude da validação dos outputs do modelo contra valores observados, método até então não considerado em abordagens anteriores.

A dificuldade de estimar as concentrações e consequentemente os estoque de C nos solos dos manguezal é ainda maior, considerando a aparente maior multiplicidade de fatores ambientais que agem em diferentes escalas (ha a Km2) (LUGO; SNEDAKER, 1974; THOM, 1982; WOODROFFE et al., 2016). A combinação de fatores regionais e de macro-escala, incluindo forçantes ambientais geofísicas (amplitude

de marés, descarga de rios) e climáticas (temperatura, precipitação, evapotranspiração), origina tipos conspícuos de ambientes geomorfológicos costeiros (coastal settings, sensu THOM, 1982). Esta heterogeneidade de ambientes determina mecanismos físico-químicos e biológicos responsáveis por variações significativas tanto na concentração e no estoque quanto nas taxas de produção subterrânea de C em múltiplas escalas (TWILLEY; RIVERA-MONROY, 2009). No capitulo 2 foi evidenciada a relevância de variáveis geofísicas e climáticas para variabilidade latitudinal da disponibilidade de nutrientes, e consequentemente da magnitude dos estoques de C em solos de manguezais. Os resultados claramente suportam a hipótese da assinatura energética de ambientes costeiros tropicais, a qual asserte que forçantes geofísicas (descarga de rios, amplitude de marés), consorciadas ao clima regional (temperatura, precipitação e evapotranspiração), determinam a biogeoquímica do solo e, consequentemente, a estrutura (área basal, altura) e função (produtividade primária) nestes sistemas. Estes resultados são importantes, pois além de serem prontamente aplicáveis a outros sistemas dominados por pulsos de inundação, considerando a similaridade estrutural e funcional de sistemas dominados por águas continentais e salobras (JUNK *et al.*, 2014; LUGO; BROWN; BRINSON, 1988; ODUM; ODUM; ODUM, 1995), urgem a necessidade de inclusão de variáveis geomorfológicas em modelos preditivos.

Figura 1 - Escalas espaciais e variáveis ambientais que influenciam a distribuição, o desenvolvimento estrutural e o funcionamento de manguezais. Extraído de WOODROFFE *et al.* (2016).
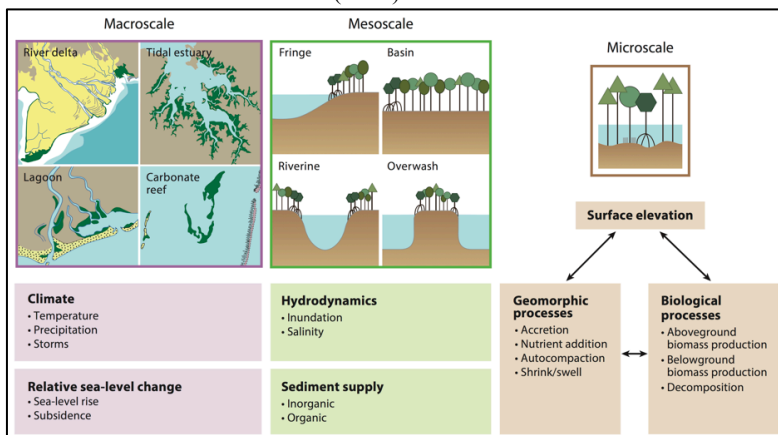
Naturalmente, o desenvolvimento de modelos robustos que buscam estimar os estoques de C em solos de manguezais em escalas regional e latitudinal está condicionado a uma malha amostral representativa dos principais tipos de ambientes geomorfológicos costeiros, ao longo de um gradiente latitudinal, bem como a disponibilidade de séries temporais de dados climáticos e geofísicos. Na atualidade, o único modelo desenvolvido com esta finalidade considera apenas variáveis climáticas, além de preditores regionais binários (i.e., presença/ausência), cuja relevância ecológica é discutível (JARDINE; SIIKAMÄKI, 2014).

Os resultados do presente trabalho sugerem fortemente que a diversidade estrutural e funcional de manguezais em macro escala é controlada por fatores geomorfológicos regionais, em contraposição a puramente gradientes climáticos de larga escala (Figura 1). Espera-se que os modelos e abordagem ora apresentados contribuam para a produção de estimativas mais precisas de C em zonas úmidas costeiras tropicais conforme preceituado por organizações internacionais de normatização e validação de inventários de carbono (p. ex., IPCC, REDD+, UNFCCC).

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