


Global impacts of projected climate changes on the extent and aboveground biomass of mangrove forests

Lidiane P. Gouvêa¹  | Ester A. Serrão¹ | Kyle Cavanaugh² | Carlos F. D. Gurgel³ | Paulo A. Horta⁴ | Jorge Assis¹

¹CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal

²Department of Geography, University of California, Los Angeles, California, USA

³Institute of Biodiversity & Sustainability, NUPEM, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil

⁴Phycology Laboratory, Department of Botany, Biological Sciences Center, Federal University of Santa Catarina, Florianópolis, Santa Catarina, Brazil

Correspondence

Lidiane P. Gouvêa, CCMAR - Centre of Marine Sciences, University of Algarve, Faro, Portugal.

Email: lidianegouv@gmail.com

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Abstract

Aim: Over the past 50 years, anthropogenic activities have led to the disappearance of approximately one-third of the world's mangrove forests and their associated ecosystem services. The synergetic combined effect of projected climate change is likely to further impact mangroves in the years to come, whether by range expansions associated with warming at higher latitudes or large-scale diebacks linked to severe droughts. We provide an estimate of future changes in the extent and aboveground biomass (AGB) of mangrove forests at global scales by considering contrasting Representative Concentration Pathway scenarios (decade 2090–2100 under RCP 2.6 in line with the Paris Agreement expectations, and RCP 8.5 of higher emissions).

Location: Global.

Methods: Boosted regression trees fitted occurrence and AGB of mangroves against high-resolution biologically meaningful data on air temperature, precipitation, wave energy, slope and distance to river Deltas.

Results: On the global scale, models produced for present-day conditions retrieved high accuracy scores and estimated a total area of 12,780,356 ha and overall biomass of 2.29 Pg, in line with previous estimates. Model projections showed poleward shifts along temperate regions, which translated into comparable gains in total area, regardless of the RCP scenario (area change RCP 2.6: 17.29%; RCP 8.5: 15.77%). However, biomass changes were dependent on the emission scenario considered, remaining stable or even increasing under RCP 2.6, or undergoing severe losses across tropical regions under RCP 8.5 (overall biomass change RCP 2.6: 12.97%; RCP 8.5: -11.51%). Such losses were particularly aggravated in countries located in the Tropical Atlantic and Eastern Pacific, and the Western and Eastern Indo-Pacific regions (regions with losses above ~20% in overall biomass).

Conclusions: Our global estimates highlight the potential effect of future climate changes on mangrove forests and how broad compliance with the Paris Agreement may counteract severe trajectories of loss. The projections made, also provided at the country level, serve as new baselines to evaluate changes in mangrove carbon sequestration and ecosystem services, strongly supporting policy-making and

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management directives, as well as to guide restoration actions considering potential future changes in niche availability.

KEYWORDS

aboveground biomass, boosted regression trees, climate change, mangrove forests, Paris agreement, representative concentration pathways

1 | INTRODUCTION

The Paris Agreement under the United Nations Sustainable Development Goals calls for adaptation and mitigation actions to reduce climate change impacts and increase the resilience of ecosystem services at global scales (Damian et al., 2018). Coastal and marine ecosystems are an important component of mitigation efforts (Gattuso et al., 2018) as they represent an effective carbon sink with the potential to absorb up to 35% of anthropogenic CO₂ emissions (Khaliwala et al., 2009). In this context, wetlands are increasingly being recognized as essential carbon sink areas (Hiraishi et al., 2014), with mangrove forests alone capturing four times more carbon than rain forests per unit area (Donato et al., 2011; Hamilton & Friess, 2018). Their mean rate of aboveground net primary production (NPP) is ~11 Mg ha⁻¹ yr⁻¹, which is in the same order of magnitude as terrestrial humid evergreen forests (10.8 Mg ha⁻¹ year⁻¹) and peat swamp forests (11.1 Mg ha⁻¹ year⁻¹; Alongi & Mukhopadhyay, 2015; Malhi et al., 2011). All carbon burial accounts for ~15% of the total organic carbon in marine environments, and this blue carbon is considered significant long-term storage (Alongi, 2015; Van Lavieren et al., 2012). Besides carbon sequestration, mangrove forests provide additional key ecosystem services (Mitra, 2020), such as protecting coastal areas from erosion and extreme weather events (Barbier et al., 2011; Doughty et al., 2016) and providing habitat and energy to associated ecological communities (Van Lavieren et al., 2012). Altogether, the financial return of mangrove ecosystem services is estimated at US\$ 194,000 ha⁻¹ year⁻¹, with a global value of US\$ 2.748 trillion year⁻¹ (Barbier et al., 2011; Costanza et al., 2014).

Over the past 50 years, anthropogenic activities, in particular deforestation, have led to the disappearance of approximately one-third of the world's mangrove forests (Valiela et al., 2001). The synergetic combined effect of climate change can increase the loss of mangroves and their ecosystem services at global scales (Ward et al., 2016). Mangroves are particularly sensitive to cold temperatures, with global distributions restricted to tropical and subtropical environments (Spalding et al., 2010). Accordingly, ongoing/projected warmer conditions have been associated with range expansions into salt marsh habitats at higher latitudes (Cavanaugh et al., 2014). The substantial part of the organic carbon reservoir of mangroves, represented by the AGB (Rovai et al., 2016), is also allocated through physiological responses to thermal conditions (Wang et al., 2021) and, therefore, with significant spatial variability throughout the globe (Giri et al., 2011; Hutchison et al., 2014). In particular, warmer conditions prevailing in subtropical regions are associated with

positive effects on the overall productivity of mangroves (Akaji et al., 2019). However, above physiological tolerance limits, thermal stress can severely impact mangroves (Field, 1995). Changes in precipitation regimes can also be detrimental (Ward et al., 2016), with large-scale diebacks recorded over the past decades associated with decreasing rainfall rates and increasing evapotranspiration (Duke et al., 2017; Field, 1995). Yet, projected changes in precipitation have substantial regional variation, and the overall patterns may increase by up to 25% (Houghton et al., 2001). Among the areas projected to have higher precipitation levels in the future, such as some Pacific Islands, increased sediment and litterfall, as well as increased nutrient inputs, may further enhance productivity (Ward et al., 2016). Meanwhile, mangroves in semi-arid areas, anticipated to have decreased future precipitation, such as the Middle East and northeast Brazil, are likely to be impacted from salt-stress and declining productivity due to reduced sediment input (Ward et al., 2016). Global sea levels are expected to rise substantially in years to come, further impacting mangroves in different ways, whether increasing soil C stores contributing to blue carbon (Chatting et al., 2022; Sasmito et al., 2016) or changing the landscape position of habitats and exposing mangroves to extreme patterns of inundation duration and frequency (Ward et al., 2016).

Carbon stored in coastal ecosystems, such as mangroves, has recently been integrated into the international policy agenda through the Paris Agreement within the United Nations Framework Convention on Climate Change. As a result, countries with mangrove forests within national boundaries need to estimate and track the amount of carbon stored in these systems. Such estimates should then be used to support well-informed decision-making and future climate change mitigation strategies. In this context, anticipating the effect of global climatic change on mangrove forests extent and AGB is crucial. There are numerous estimates of mangrove extent and biomass levels for present-day conditions, which vary between 13,000,000 and 24,000,000 ha (Giri et al., 2011; Spalding et al., 2010; Twilley et al., 1992) and 1.52 and 2.83 Pg (Hutchison et al., 2014; Hu et al., 2020); however, no such attempt has been made for future conditions on the global scale. The present study uses a machine learning framework tuned with high-resolution predictor variables and empirical data on the distribution and biomass levels (e.g., Gouvêa et al., 2020) to estimate future changes in mangrove forest extent and AGB under contrasting Representative Concentration Pathway scenarios (decade 2090–2100 under RCP 2.6, in line with the Paris Agreement expectations, and RCP 8.5, of increased emission of greenhouse gas). These estimates are provided at the global

scale and country levels and serve as new baselines to evaluate and track changes in mangrove carbon sequestration and ecosystem services, aligned with policy requirements guiding conservation priorities, and to account for future changes in niche availability while planning restoration actions.

2 | METHODS

A comprehensive dataset describing the global distribution of mangrove forests was downloaded from the United Nations Environment World Conservation Monitoring Centre. This dataset provides occurrence records compiled from earth observation satellite imagery by Giri et al. (2011) updated by UNEP-WCMC (version 1.4, March 2021) and has been widely used to explore the relationship between climate changes and distributional range shifts of mangrove forests (He et al., 2022; Peereman et al., 2022), thus allowing proper comparisons between additional estimates. Empirical AGB data covering the overall distribution of mangrove forests were gathered from the available literature and Rovai et al. (2016) dataset (Table 1; Figure S1). Studies were compiled through the Web of Science with the searching criteria of “mangrove” and “above-ground biomass,” and only those reporting geographic coordinates and/or location names were considered.

Six environmental data layers were downloaded from Bio-ORACLE 2 (Assis et al., 2018; Tyberghein et al., 2012) for present-day conditions (from 2000 to 2017) and the two contrasting RCP scenarios (RCP 2.6 and RCP 8.5; decade 2090–2100), namely, air surface temperatures (long-term average of monthly maximum and minimum), precipitation, slope, wave energy and distance to river Delta. The choice of these layers was based on the biological relevance of mangrove forests. Specifically, mangroves are known to thrive in regions with warm temperatures and high humidity levels (Osland et al., 2017). Nevertheless, temperatures above extreme thresholds can produce losses in AGB levels (Field 1995, Ward et al., 2016). Additional drivers, including smoothly sloping intertidal areas associated with bays, lagoons, estuaries and deltas (Leong et al., 2018; Schaeffer-Novelli et al., 2016), as well as low wave energy conditions, can also be important to the establishment and growth of mangroves (Amm & Bhaskaran, 2020; Sánchez-Núñez et al., 2019). The Bio-ORACLE 2 layers are made available at a spatial resolution of 5 arcmin resolution (~9.2 km); those for RCP consider the ensemble of the general atmosphere–ocean circulation models CCSM4, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-LR and MIROC-ESM processing detailed by Assis et al. (2017). Prior to modelling, Pearson's correlation coefficient and variance inflation factor (VIF) was estimated between predictors.

The machine learning algorithm Boosted Regression Trees (BRT) was chosen to model the distribution and AGB of mangroves since it handles nonlinear relationships and complex interactions and systematically retrieves high predictive performances (Elith et al., 2008). Modelling was based on a two-phase approach: (1) the development of a distribution model to estimate the global extent of

mangroves by fitting mangrove occurrence records against the environmental predictors with a “Bernoulli” and (2) the development of a biomass model fitting AGB data and the predictors with a “Gaussian” distribution. The models were performed based on the aggregation of data from multiple mangrove taxa with similar functional forms in order to capture the niche of the whole biome (e.g., Jayathilake & Costello, 2018, 2020). This approach, also known as “community-level” modelling, can accommodate data-poor regions for particular taxa (D'Amen et al., 2017; Smith et al., 2019).

To remove surplus information and reduce (Di Cola et al., 2016) the potential effect of spatial autocorrelation in the distribution model (Segurado et al., 2006), records were gridded to the spatial resolution of the climatic layers, and duplicate occurrences were removed. Additionally, a spatial autocorrelation function, as described by Di Cola et al. (2016), was used to select one presence record only within the distance estimated as significantly autocorrelated. Additionally, due to the lack of absence data for the distribution model (presence-only modelling), pseudo-absences were randomly generated in a 1:1 ratio with presence data, except in the locations where mangrove forests occur. This allows improving the performance of BRT models while isolating potentially contributive predictors (Barbet-Massin et al., 2012; Cerasoli et al., 2017). Biomass data were averaged in the specific cases of multiple records falling within the same cells of the environmental predictors. This process might not have strongly impacted the biomass values found in the same cells because variability (at the cell scale) was generally low (326 records averaged into 171 cells with an average coefficient of variation of 1.01 t ha^{-1}).

A cross-validation framework using spatial blocks with 10 random folds was implemented in both occurrence and biomass models based on the method described by Valavi et al. (2019). The use of spatial blocks allowed generating independent data to properly assess the predictive performance of models and error estimation (Roberts et al., 2017; Valavi et al., 2019), here aimed for the selection of the optimal BRT hyperparameters (Elith et al., 2008). In this process, all parameter combinations (i.e., the “grid search” method) of tree complexity (1–6), number of trees (50–1000, step 50) and learning rate (0.01–0.001, step 0.001) were used to train models with nine folds of data, while one independent fold was withheld at a time (Figure S2) to test the performance of models with the Boyce index for the distribution model (see details below) and deviance explained for the biomass model. Monotonicity constraints were further implemented to reduce overfitting and improve the transferability of models (Hofner et al., 2011). These were based on the expected outcomes of each predictor variable on the response of models, as documented in the literature. Specifically, we hypothesize that minimum temperature and precipitation have a positive effect on mangrove occurrence and AGB and, that maximum temperature, slope, wave energy and distance to Delta have a negative effect (Cannon et al., 2020; Friess et al., 2022).

The performance of the distribution model was reported with the Boyce index, particularly suitable for presence-only modelling (Boyce et al., 2002), and the area under the receiver operating characteristic

curve (AUC). The Boyce index varies between -1 to $+1$, and the AUC index between 0 and 1. Negative values of the Boyce index, or close to zero of the AUC index, indicate incorrect model predictions. Boyce index values above zero, or AUC values above 0.5, indicate predictions better than random, while values of both indices close to 1 indicate predictions consistent with the distribution of presence records (Hirzel et al., 2006). The performance of the biomass model was reported with deviance explained and by plotting observed versus predicted AGB values. The ecological significance of the models was investigated by determining the contribution of each predictor to the performance of models and by developing partial dependency plots, from which tipping points reflecting extreme conditions to occurrence and biomass were extracted (Elith et al., 2008).

Global distribution estimates in terms of area and AGB were produced for present-day conditions and the two RCP scenarios both as maps and summary tables aggregating results per marine realm (Spalding et al., 2007) and Economic Exclusive Zone (EEZ). In this process, predictions from the distribution model were reclassified to binomial responses using a threshold allowing to maximize the agreement between observed and predicted occurrence records (i.e., maximization of true skill statistics, e.g., Allouche et al., 2006). Predictions from the biomass model were restricted to the regions where the distribution model estimated the presence of mangroves and to the maximum observed AGB value to remove potential model extrapolation (e.g., Carvalho et al., 2019; Barry & Welsh, 2002). Finally, because the resolution of environmental data used in the modelling can lead to predictions of suitable areas beyond the coastal distribution of mangroves, we implemented a post-filtering process, as described by Fournier et al. (2017). This refined the outputs of the models, i.e., predictions considering the effect of continental scale environmental conditions, according to a habitat filter at relevant local scales (Fournier et al., 2017). Specifically, a habitat filter was developed with the high-resolution (15 arc-second, approximately 450 meters) General Bathymetric Chart of the Oceans (GEBCO, 2019) considering only altimetry/bathymetry values within the hydrographic zero, i.e., the lowest level of astronomical tides, and the maximum annual tidal amplitude per gridded cell (e.g., Assis et al., 2014). This process allowed restricting predictions to realistic coastal areas where mangroves might occur, thus reducing potential area overestimations (Fournier et al., 2017) and also to consider the potential add-on effect of projected sea-level rise. In particular, future projections took the hydrographic zero 0.45 m higher than present-day conditions for RCP 2.6 and 0.93 m higher for RCP 8.5 (Horton et al., 2020).

All analyses were performed in R (R Development Core Team, 2018) and RStudio v.3.6.6 (R Core Team, 2018). All data and code are openly available (please refer to the data availability statement).

3 | RESULTS

Occurrence data compilation and processing (after removing duplicates and implementing spatial autocorrelation constraints over the

initial 20,016 records) resulted in 4806 records (plus 4806 pseudo-absence records) to model the global distribution of mangroves (Figure S3) and in 109 records to model AGB (Table 1; Figure S1). The AGB records varied between 4.3 and 808.96 t ha⁻¹, with an average of 166.34 ± 166.21 t ha⁻¹, with studies sampling 4.20 ± 8.98 sites on average (range between 3 and 92 sites). The distribution model retrieved high predictive performance (cross-validation Boyce index: 0.78 ± 0.19 ; final prediction Boyce index: 0.99; final prediction AUC: 0.97) and matched the known distribution of mangroves at global scales, as detailed in additional studies (Giri et al., 2011; Hutchinson et al., 2014; Hu et al., 2020; Figure 1). The biomass model showed little deviation between observed and predicted values (CV deviance explained: 0.61 ± 0.04 ; final model deviance explained: 0.81, Figure 2), resulting in a mean error of 1.00 ± 1.58 t ha⁻¹.

Minimum temperature largely explained the occurrence of mangroves (relative contribution of 74.38%), followed by precipitation and slope (combined contribution of 19.37%; Figure 3). For Biomass, precipitation and maximum temperature were particularly important (combined contribution of 53.03%), followed by wave energy, distance to delta, and minimum temperature (Figure 3). These results are supported by the generally low correlation found between predictor layers. Only temperature predictors showed a stronger correlation (Pearson's correlation 0.90; VIF > 5; Figure S4; Table S2), yet their opposite fit, as forced by monotonicity constraints, removed potential confounding inferences regarding their contributions to the response of models. Considering the most contributive predictors, conditions for the occurrence of mangroves were predicted with temperature above 11.73°C, precipitation above 121.67 mm yr⁻¹ and reduced terrain profiles of slope lower than 6.35° (Figures 3 and S5). Increased AGB values were predicted with temperatures between 13.4 and 30.9°C, precipitation above 292 mm yr⁻¹, wave energy below 3.1 and distances to deltas lower than 3683 km (Figures 3 and S6).

For present-day conditions, models estimated a total area of 12,780,356 ha and a mean and overall AGB of 179.29 t ha⁻¹ and 2.29 Pg, respectively. Approximately 90% of the predicted mangrove extent and biomass were estimated in Tropical Atlantic and the Western and Central Indo-Pacific (Table 1). The models considering the two RCP scenarios of future change projected similar distribution areas of 14,953,016 and 14,697,409 ha (RCP 2.6 and RCP 8.5, respectively), corresponding to increases of 17.29% and 15.77% when compared with the present (Table 1). These changes were mostly driven by poleward shifts along the temperate coastlines of the Southern Africa, Northern Pacific, South America, and Northern Atlantic (Table 1), at a projected rate of 8.04 and 32.37 km per decade (RCP 2.6 and RCP 8.5, respectively). Area losses of 28.01% and 43.49% were projected in the Tropical Eastern Pacific and Eastern Indo-Pacific, respectively (Figure 4; Table 1).

Future estimates of mean AGB varied between 171.75 and 136.61 t ha⁻¹, corresponding to 4.20% and 23.80% (Table 1). When combined with distribution estimates, these changes translated into overall biomass changes highly dependent on the emission scenario considered, remaining stable or even increasing under RCP 2.6, or

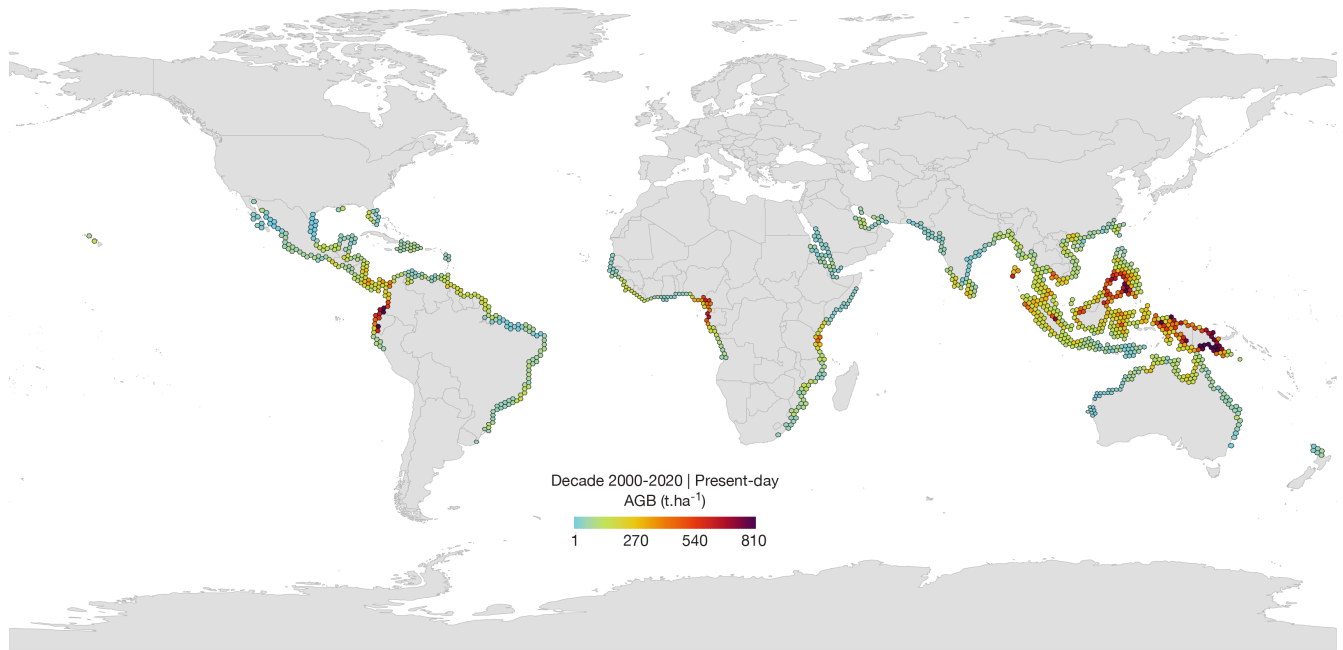


FIGURE 1 Potential distribution and aboveground biomass of mangrove forests predicted for present-day conditions at global scales. Map aggregated to equal-size polygons for better visualization.

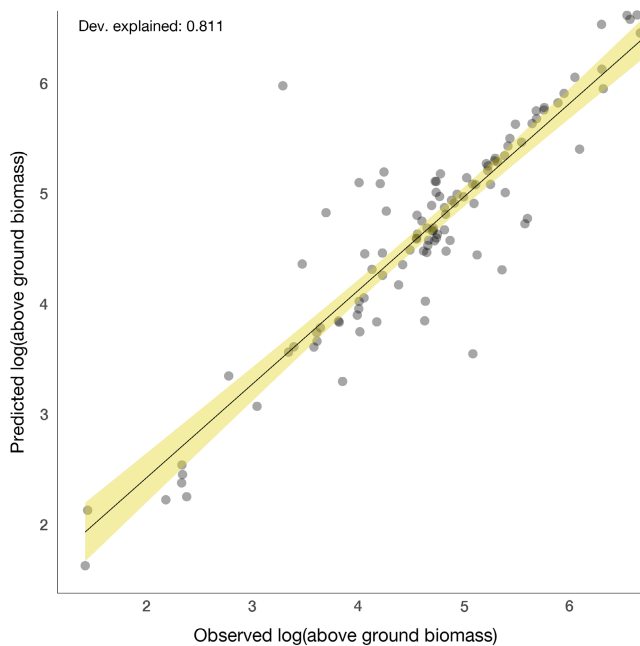


FIGURE 2 Relationship between observed and predicted biomass of mangrove forests (nature logarithm of aboveground biomass as $\text{t}\cdot\text{ha}^{-1}$; deviance explained: 0.811).

experiencing losses across all tropical regions under RCP 8.5 (overall biomass change RCP 2.6: 12.97%; RCP 8.5: -11.51%), particularly severe in the Tropical Atlantic, Eastern Pacific, and Western and Eastern Indo-Pacific (global losses above ~20% in overall biomass; Table 1). Countries like Brazil, Colombia, Ecuador, Guyana, Guinea, Mozambique, Sierra Leone and Suriname, predicted to have higher present-day overall biomass levels (>5 million tons), are expected

to be severely impacted under RCP 8.5 (losses >75% in overall biomass; Table S3) owing to increased warming conditions (average temperature increase of $3.69 \pm 0.22^\circ\text{C}$; Table S3) and reduced habitat availability due to sea level rise (average habitat reduction of $-178,875 \pm 186,189$ ha; Table S3). Among these countries, Suriname, Guyana, Guinea and Mozambique are further projected to undergo future reductions in precipitation (average precipitation reduction of -1.07 ± 0.75 $\text{mm}\cdot\text{yr}^{-1}$; Table S3). Additional estimates at the country level (i.e., per Economic Exclusive Zones) are available in Table S3.

4 | DISCUSSION

Modelled projections for the period 2090–2100 estimate poleward range expansions along temperate regions, and changes in overall biomass levels, particularly intensified under the higher emission scenario RCP 8.5. Following the Paris Agreement expectations, reduced environmental changes (e.g., temperature and precipitation regimes), coupled with local scale habitat availability, may add up 17.29% in global mangrove area and 12.97% in overall biomass, while more drastic environmental changes owing to the continuous / intensification of greenhouse gas emissions may severely impact the overall biomass of mangroves, with losses of 11.51%, which add up to the already lost mangroves over the past 50 years, estimated in approximately one-third when compared with past distributions (Valiela et al., 2001). Projected changes were particularly striking along the Tropical Atlantic, Eastern Pacific, and Western and Eastern Indo-Pacific, severely impacting countries like Brazil, Colombia, Ecuador, Guyana, Guinea, Mozambique, Sierra Leone and Suriname. These novel estimates, supporting policy-making

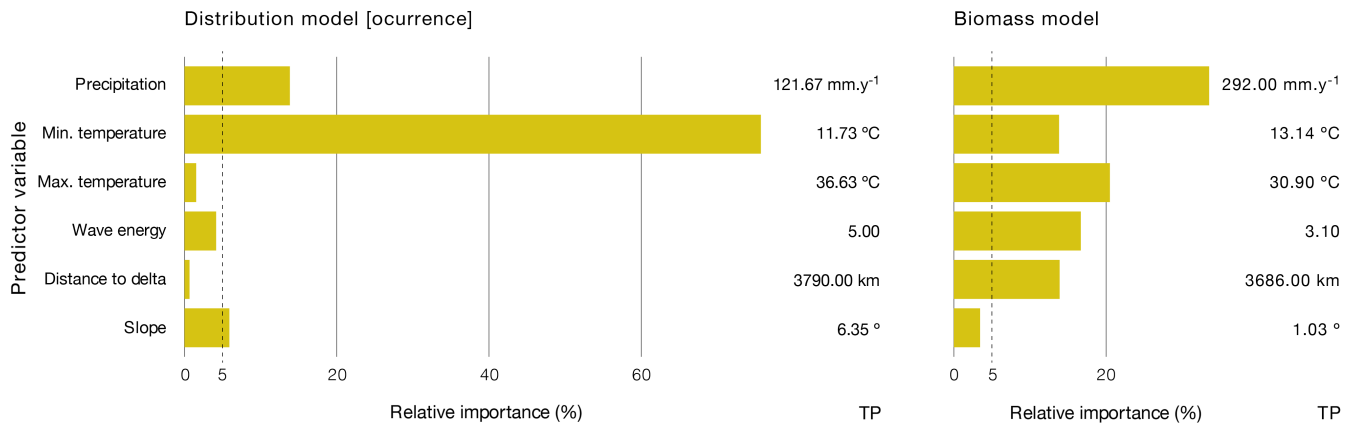


FIGURE 3 Relative contribution (%) of predictor variables to the (left) distribution and (right) biomass models. Dotted lines depict a contribution threshold of 5%. Tipping points shown represent values from which the models predicted the occurrence or biomass of mangroves.

TABLE 1 Potential distribution areas, average and overall biomass of mangrove forests predicted per marine realm according to Spalding et al. (2007) for the present and future (decade 2090–2100) representative concentration scenarios (RCP).

Realm	Area (ha)			Average biomass (t ha ⁻¹)			Overall biomass (t)		
	Present	Changes (%)		Present	Changes (%)		Present	Changes (%)	
		RCP 2.6	RCP 8.5		RCP 2.6	RCP 8.5		RCP 2.6	RCP 8.5
Temperate Southern Africa	10,588	+37.46	+78.72	45.57	-12.42	-26.60	482,509	+20.39	+31.18
Temperate Northern Pacific	243,412	+57.11	+52.40	40.12	-17.18	-14.86	9,765,281	+30.11	+29.75
Tropical Atlantic	2,897,646	+23.41	+19.10	125.40	-15.76	-44.61	363,372,631	+3.96	-34.03
Western Indo-Pacific	3,079,100	+11.59	+6.86	110.33	-4.79	-24.57	339,718,943	+6.25	-19.39
Temperate South America	105,736	+113.03	+234.88	60.46	-8.87	-55.37	6,392,924	+94.12	+49.46
Central Indo-Pacific	5,669,813	+14.16	+6.22	232.77	-0.95	-14.15	1,319,755,150	+13.08	-8.81
Temperate Northern Atlantic	97,713	+99.00	+624.14	23.77	+52.11	+77.17	2,322,239	+202.72	+1182.98
Temperate Australasia	132,150	+8.83	+43.37	37.53	-0.36	-20.09	4,959,377	+8.44	+14.56
Tropical Eastern Pacific	542,288	-0.10	-28.01	249.67	+1.21	-31.61	135,394,967	+1.11	-50.76
Eastern Indo-Pacific	1910	+91.31	-43.49	109.15	-85.57	-78.57	208,451	-72.39	-87.89
Global	12,780,356	+17.29	+15.77	179.29	-4.20	-23.80	2,291,418,861	+12.97	-11.51

Note: Areas (ha), average biomass (t ha⁻¹), overall biomass (t) and changes (%) according to RCP scenarios are shown. The minus and plus signs represent areas with losses and gains of mangrove forests, respectively.

and management directives, highlight the potential effect of future climate change on global mangrove forests and how broad compliance with the Paris Agreement may counteract trajectories of change.

The models predicting for present-day conditions matched the known distribution of mangroves at global scales (i.e., throughout the Tropical Atlantic and the Western and Central Indo-Pacific) and displayed reduced deviance with the observed AGB data (~80% of variability explained). The provided estimates of area and biomass of 12,780,356 ha and 2.29 Pg, respectively, are in line with the additional estimates reported of 13,042,000/13,065,675 ha (Hu et al., 2020; Tang et al., 2018) and 1.91/2.83 Pg (Hutchison

et al., 2014; Tang et al., 2018). In particular, the implemented approach of “community-level” modelling (D’Amen et al., 2017) allowed capturing the niche of the whole biome (e.g., Jayathilake & Costello, 2018, 2020), which could be precluded by a species-by-species approach, considering the potentially scarce information in unsampled or overlooked regions (e.g., Brazil and Africa regions). Additional studies using satellite tools have also estimated mangrove distributions at the community level and achieved similar results to ours, in line with mangroves’ empirical occurrence (Giri et al., 2011; Hutchinson et al., 2014; Hu et al., 2020). But despite the overall agreement found, differences are expected between studies owing to different methods used (Hu et al., 2020), and overprediction is

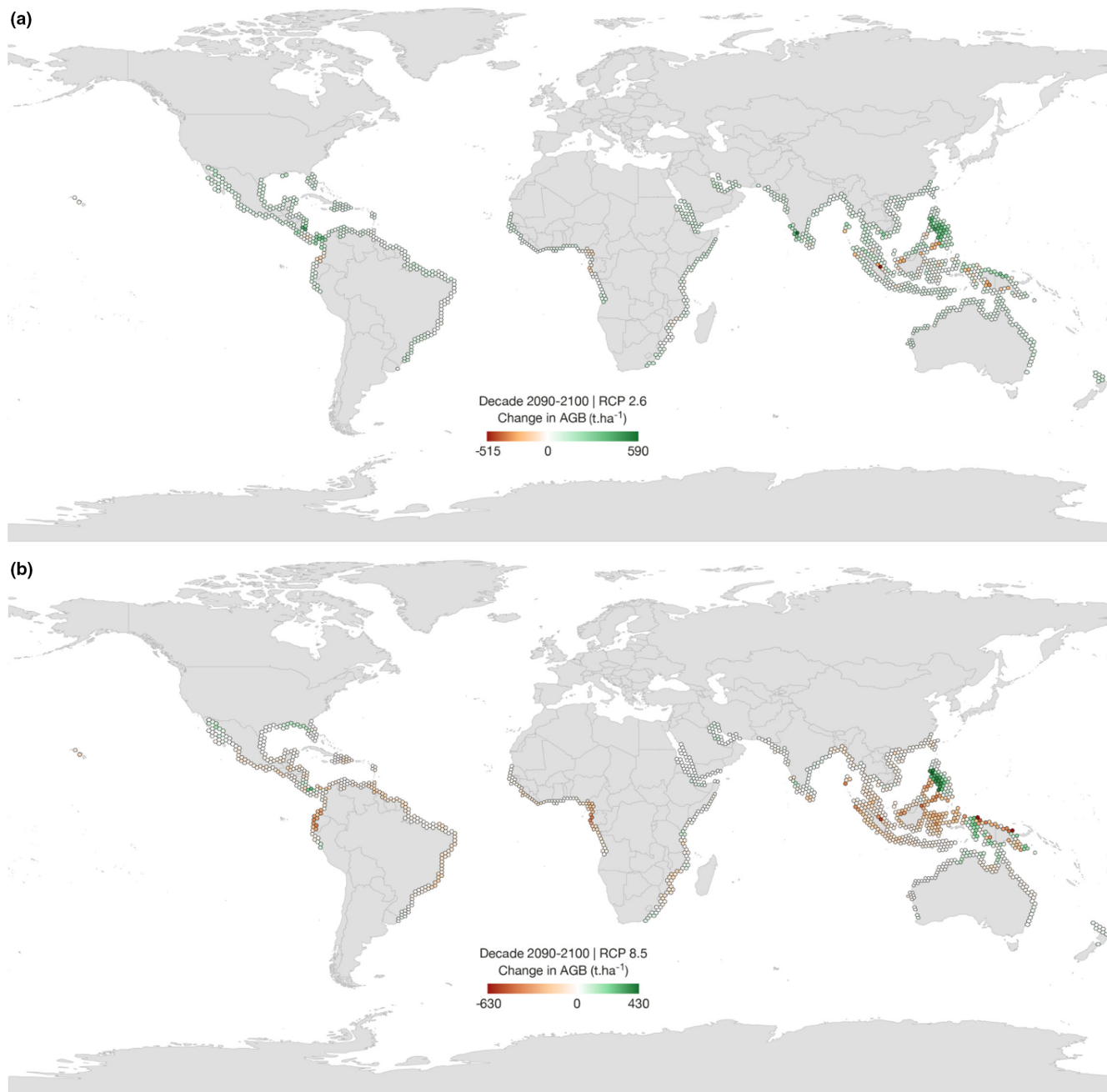


FIGURE 4 Change in potential distribution and aboveground biomass projected for mangrove forests (from 2000–2017 to 2090–2100) under the (a) RCP 2.6 and (b) RCP 8.5 scenarios of climate change. Maps aggregated to equal-size polygons for better visualization.

somewhat inherent to our approach, as predicted estimates result from areas with environmentally suitable conditions, where mangroves may not currently occur owing to additional factors (e.g., human-induced deforestation). Throughout the regions predicted as suitable for mangroves to thrive, biomass varied significantly, with average observed values of $166.34 \pm 166.21 \text{ t.ha}^{-1}$, similar to predicted values of $179.29 \pm 181.40 \text{ t.ha}^{-1}$. Biomass estimates were particularly high in the Central Indo-Pacific, accounting for almost half of the total global AGB (Hutchison et al., 2014). This is also the region with the highest diversity of mangroves at global scales (Suratman, 2008).

The modelled patterns of mangroves' distribution were mostly explained by minimum air temperature and precipitation, while those of biomass accounted for the additional contribution of maximum temperature. Suitable conditions for mangroves' occurrence were predicted with temperatures and precipitation levels above 11.73°C and $121.67 \text{ mm.yr}^{-1}$, respectively, while increasing biomass was predicted with temperatures and precipitation above 13.14°C and 292 mm.yr^{-1} , reaching an optimum state with levels of 25.75°C and 730 mm.yr^{-1} (Figure S6). Similar thresholds were empirically observed elsewhere (Field, 1995; Osland et al., 2017). Regarding temperature, studies have reported min air temperatures for occurrence

above 13.5°C, with some species tolerating colder environments, such as *Avicennia germinans* in the subtropical northern Gulf of Mexico (Cavanaugh et al., 2018; Madrid et al., 2014) and higher productivity levels from 15 to 25°C (Hutchings & Saenger, 1987). Physiological damage has been observed at temperatures exceeding 34°C, with photosynthetic rates falling close to zero at 38 and 40°C (e.g., Andrews & Muller, 1985; Cheeseman et al., 1991; Field, 1995). Regarding precipitation, studies have shown mangroves occurring in sub/semi-humid and arid areas experiencing low precipitation rates ranging between 320 and 780 mm.yr⁻¹ (Alongi, 2009; Quisthoudt et al., 2012; Osland et al., 2017). Non-climatic drivers were also included in the models, such as slope, wave energy and distance to major river delta, as the establishment of mangrove forests is further dependent on smoothly sloping intertidal areas in association with bays, lagoons, estuaries and deltas, of low wave energy conditions (Leong et al., 2018; Schaeffer-Novelli et al., 2002). The lack of a continental shelf and irregular relief can prevent mangrove occurrences (Ward et al., 2016). Additionally, the low wave energy (Amm & Bhaskaran, 2020) and distance to the river delta also emphasize that mangroves need not only protected regions from precluding soil erosion but also favourable nutrient conditions for tree growth. However, these predictors had a residual contribution to the model when compared with temperature and precipitation (as verified elsewhere; Record et al., 2013).

The models allowed to project for the first time the future extent and biomass of mangroves at global scales. Poleward range shifts were projected in temperate regions regardless of the scenario considered, in line with additional studies already reporting the expansion of mangrove forests (Almahasheer et al., 2016; Cavanaugh et al., 2014; Coldren et al., 2019; Osland et al., 2019). These shifts have been attributed to the reduction in cold temperature conditions and freezing events, as well as to changes in precipitation regimes (Cavanaugh et al., 2014; Saintilan et al., 2014), corroborating our modelling expectations of higher probability of occurrence with increasing levels of the two predictors. Overall, projections showed a positive trend in the future extent of mangroves, yet biomass was largely dependent on the emission scenario considered and showed high spatial variability. While countries like Fiji, Madagascar, New Zealand, Solomon Islands and Somali may strongly increase biomass levels (gains in biomass above 50%; Table S3) owing to increased precipitation levels (positive anomaly in precipitation under RCP 8.5; Table S3), the general trend under the higher emission scenario is of severe losses, strongly impacting mangroves in countries located in the Tropical Atlantic, Eastern Pacific, and the Western and Eastern Indo-Pacific regions. In the same way, ongoing reports align with our future projections, showing climate-induced expansions of mangroves in temperate regions, diebacks and biomass losses are also being reported across the tropics (Barros & Albernaz, 2014; Clausen et al., 2010; Lovelock & Ellison, 2007; Shearman, 2010) owing to warmer conditions (Ward et al., 2016; Friess et al., 2022) and decreasing rainfall rates (Alongi, 2015; Duke et al., 2007; Ward et al., 2016; Wilson, 2017). For instance, the harsh conditions in which mangroves can potentially survive, as predicted for some

regions by our models, means that any slight increase in temperature and aridity levels (Figures S7 and S8) may result in severe and potentially irreversible mangrove changes (Adame et al., 2021).

Despite the high performance of our models, the overall approach has some limitations that should be acknowledged. First, it is important to recognize that the models considered only the potential impacts of climate change on the distribution and biomass of mangroves. Other anthropogenic drivers such as deforestation, hydrology alterations, CO₂ enrichment and pollution may overwhelm the effects of climate change in some areas. Over the past decade, the global rate of mangrove losses has decreased, however, such disturbances are still major threats in some countries, and restoration efforts have had mixed results (Friess et al., 2022; Goldberg et al., 2020). Second, the conversion of probability estimates (the first output of models) into binomial maps may have degraded the information of predictions (Guillera-Arroita et al., 2015). Ideally, models should provide a perfect discrimination of presences and absences, ultimately leading to binomial maps depicting the true occurrence of mangroves. But potential data limitations and stochasticity in mangroves' occupancy can preclude the use of thresholds reclassifying probabilistic predictions of species occurrence (Guillera-Arroita et al., 2015). Here, the use of a compressive dataset of occurrence records aggregated at the 'community-level' (D'Amen et al., 2017) may have proved beneficial, producing models with high performance, and mimicking the actual distribution of mangroves; nevertheless, probabilistic prediction layers are provided (please refer to data availability statement). Third, projecting the impacts of climate change can be a challenging task due to the lack of observations supporting predictions (Elith et al., 2008). Also, there is a risk of extrapolating to climatic conditions not yet occurring in the present (Elith et al., 2008). This may have occurred in our projections with temperatures above ~40°C (Figure S5), potentially occurring in the Persian Gulf and the Gulf of Oman (Figure S9). Fourth, the models did not consider constraints on the ability of mangroves to migrate inland with sea level rise (e.g., anthropogenic barriers), which are likely to have a significant impact on future changes in mangrove areas (Schuerch et al., 2018). The estimates considered sea level changes through a post-filtering technique (Fournier et al., 2017), but the mangrove's ability to perform vertical accretion can be precluded if changes exceed 6.1 mm.yr⁻¹ (Saintilan et al., 2020), which translates to 0.49 m by the end of the century, largely surpassing the RCP 8.5 threshold of 0.93 m (Horton et al., 2020). Furthermore, for passive dispersal species, like mangroves that are highly dependent on the patterns of ocean currents, oceanographic barriers may block the expansions projected along temperate regions (Molinos et al., 2017).

Overall, our global estimates highlight the potential effect of future climate changes on mangrove forests. If broad compliance with the Paris Agreement fails, severe mangrove losses may occur in tropical regions, as already reported elsewhere. Such losses will likely impact the multiple ecosystem services provided, importantly, the role in carbon sequestration (Howard et al., 2017). Losses may also increase greenhouse gas emissions, and centuries to millennia of accumulated carbon can be released in a short period. For instance, the recent loss of ~35,000 km² of mangrove coverage is expected

to continue emitting 0.07 Gt CO₂ over the next decades (Crooks et al., 2011).

The identification of vulnerable regions/ countries to future climatic impacts under contrasting scenarios of global change serves as new baselines to evaluate changes in carbon sequestration, strongly supporting international policy agendas, the Paris Agreement, within the United Nations Framework Convention on Climate Change. In this scope, the Intergovernmental Panel on Climate Change highlights the need to provide estimates with the lowest possible uncertainty. Here, our models predicting occurrence and biomass with high performance do so. Additionally, effective conservation planning, decision-making, and mitigation strategies can now be climatically informed (Mcleod & Salm, 2006) with our projections stressing the urgent need for initiatives conserving blue carbon (Taillardat et al., 2018), as evidence shows more effective sequestration and reduced losses in intact mangroves areas (Miteva et al., 2015; Nam et al., 2016). The establishment of climate-smart networks of marine protected areas may be the way, particularly relevant in the scope of the new post-2020 Global Biodiversity framework.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Occurrence data, environmental layers, R code, ODMAP protocol and the predictions made under contrasting climate change conditions are openly available in fig share at: <https://doi.org/10.6084/m9.figshare.20152445>.

PEER REVIEW

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ORCID

Lidiane P. Gouvêa  <https://orcid.org/0000-0001-7010-5500>

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BIOSKETCH

Lidiane P. Gouvêa is a biologist with PhD in ecology focused on how climate-driven distributional shifts can impact coastal and marine species.

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SUPPORTING INFORMATION

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