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Global relationship between upwelling intensities and mangrove distribution and area

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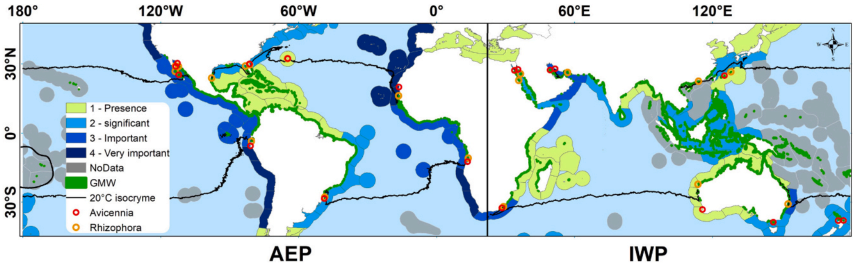
HIGHLIGHTS

- Upwelling systems are found at mangrove range limits.
- Mangrove areas peak are in low upwelling intensities.
- Upwelling varies across mangrove bioregions
- High upwelling yields sparse mangroves

GRAPHICAL ABSTRACT



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ABSTRACT

Mangroves are essential coastal ecosystems distributed across tropical and subtropical regions, typically found at the confluence of river systems and the sea. Although air temperature has long been recognised as a key determinant of mangrove distribution, upwelling systems that transport cold, nutrient-rich waters from the deep ocean to the surface can also impede mangrove propagule dispersion. However, global studies that examine the influence of upwelling on mangrove distribution remain scarce. In this study, our objective was to investigate the relationship between upwelling systems and global mangrove distribution, with an emphasis on range limits and area extent. We adopted a novel multi-scale approach by analysing mangrove areas at several minimum size thresholds ($\geq$5 ha, $\geq$50 ha, $\geq$100 ha, $\geq$200 ha, and $\geq$ 300 ha) to evaluate the scale dependence of upwelling effects. Our regression models revealed a clear trend: the coefficient of determination (R^2) increased from 0.20 for patches $\geq$5 ha to 0.37 for $\geq$50 ha, 0.43 for $\geq$100 ha, 0.49 for $\geq$200 ha, and reached 0.53 for patches $\geq$300 ha. Furthermore, low-upwelling regions harbour 47.7 % of the total mangrove area (66,763 km^2), whereas high-upwelling regions account for only 0.5 % (2642 km^2). We also found that the highest upwelling intensities occur exclusively in the Atlantic East Pacific mangrove region, a key environmental contrast to the Indo-West Pacific. In conclusion, our study demonstrates that upwelling systems are one factor shaping global mangrove distribution in a strongly scale-dependent manner, with larger, contiguous patches exhibiting a markedly

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stronger response. These insights emphasise the need to incorporate upwelling intensity and spatial scale into global mangrove conservation and management strategies. This integration is essential to address the complex interplay of environmental factors under shifting oceanographic and climatic conditions.

1. Introduction

Mangrove ecosystems occur worldwide along tropical and subtropical coastlines. They are located at the land-sea interface and are influenced by terrestrial and oceanographic abiotic factors (Tomlinson, 2016). The world mangrove distribution is delimited at approximately 30° latitude on either side of the equator, with a few exceptions (Duke, 1992; Duke et al., 1998; Giri et al., 2011; Bunting et al., 2022). For many years, two central questions regarding the global distribution of mangroves have intrigued researchers: What limits their range? and What restricts their expansion? (Quisthoudt, 2013; Duke et al., 1998; Osland et al., 2017a; Ximenes et al., 2021, 2023).

Historically, sea surface temperature (SST) was considered the primary determinant of mangrove distribution (Barth, 1982; Hutchings and Saenger, 1987; Woodroffe and Grindrod, 1991; Duke et al., 1998). However, a multifactorial framework is now recognised, in which minimum air temperature, precipitation, and other climatic variables also play pivotal roles (Saenger, 2002; Duke, 2006; Semeniuk, 2013; Osland et al., 2017a, 2017b; Cavanaugh et al., 2018; Ximenes et al., 2021). Mangrove species are particularly sensitive to cold, with distribution limits evident in regions such as China and North America (Chen et al., 2017; Wu et al., 2018; Stuart et al., 2007; Cavanaugh et al., 2014; Osland et al., 2017a). While the role of SST in defining mangrove range is well documented, the influence of low SST on propagule establishment and dispersal is less understood (McMillan, 1971; Steinke and Naidoo, 1991; Ximenes et al., 2018). Different species have different temperature requirements, like in *Avicennia marina* and *Avicennia schaueriana*. Other species, like *Laguncularia racemosa*, can handle lower temperatures better (Steinke and Naidoo, 1991; Oliveira, 2005; Santos Borges et al., 2019). Another study suggest that water temperature thresholds are species-specific and critical for understanding mangrove distribution and abundance (Li et al., 2024).

Upwelling events driven by coastal divergence due to Ekman transport, bring cold, nutrient-rich waters to the surface (Smith, 1968). Prevailing Wind stress and Earth's rotation cause surface waters to move 90° to the right in the northern hemisphere and to the left in the southern hemisphere, allowing deep waters to rise (Smith, 1968). While this enhances nutrient availability (e.g. Fréon et al., 2009), it also cools surface waters, which can inhibit mangrove seedling growth. High upwelling intensities decrease sea surface temperatures (SST) by 3 °C to 8 °C, depending on site-specific and seasonal factors (Guimaraens and Coutinho, 1996; Campos et al., 2013), and extreme cases, such as along Florida's coast, can drop SST by up to 11 °C in ten days (Pitts and Smith, 1997).

Globally, upwelling varies in intensity and spatial extent (Wang et al., 2015), and is influenced by large-scale phenomena like El Niño, which suppresses upwelling in areas such as the Peruvian coast. Four major high-intensity coastal upwelling systems are linked to EBC, which close subtropical gyres in ocean basins. These systems, known as Eastern Boundary Upwelling Ecosystems (EBUEs), significantly affect marine species distributions (Fréon et al., 2009), with upwelling events playing crucial roles in shaping ecosystems globally (Guimaraens and Coutinho, 1996; Macpherson, 2002; Fréon et al., 2009; Trainer et al., 2010; Menge and Menge, 2013; Armbrecht et al., 2014; Fenberg et al., 2015; Lourenço et al., 2016). These upwelling systems affect mangrove distributions both directly through low SST and indirectly by inducing aridity. For example, seasonal upwelling in the northern Arabian Sea contributes to coastal aridity (Lacerda, 2002), and upwelling zones coincide with mangrove distribution limits along the southwestern coast of Africa (Benguela Upwelling), the western coast of Australia, and South America's western coast (Humboldt Current) (Chapman, 1975).

High-intensity upwelling events in the Peruvian coast, linked to the Humboldt Current, restrict mangroves (Woodroffe and Grindrod, 1991; Lacerda and Schaeffer-Novelli, 1999), and upwelling associated with the California Current affects mangrove limits (Lacerda, 2002). In Brazil, the eastern limit of South American mangroves is at approximately 28°30′S latitude (Schaeffer-Novelli et al., 1990; Soares et al., 2012). Among various factors affecting mangrove distribution, upwelling is likely an additional process influencing the survival of propagules dispersed southward by the Brazil Current, particularly during spring and summer when this area experiences stronger localised upwelling (Campos et al., 2013; Ximenes et al., 2021). The pronounced gradient between air and water temperatures in upwelling zones is an important factor influencing species-specific responses to upwelling intensity. This differential effect may explain the varied impacts of upwelling on mangrove species and their distributions (Li et al., 2024). Despite growing recognition of upwelling's role in mangrove ecosystems, the global relationship between upwelling systems and mangrove distributions remains underexplored (Chapman, 1975; Li et al., 2022a, 2022b).

This study aims to evaluate the global relationship between upwelling events and mangrove distribution, with a particular emphasis on how upwelling intensities influence mangrove range limits and spatial extent. Specifically, we address the following questions: (i) Is there a spatial correlation between mangrove range limits and upwelling systems? (ii) Do mangrove area extents vary across different upwelling intensities? (iii) Are there discernible differences in upwelling intensities between the two major mangrove biogeographic regions, the Atlantic East Pacific (AEP) and the Indo-West Pacific (IWP)?

We hypothesise that regions characterised by lower upwelling intensities will support larger and more contiguous mangrove areas, as higher sea surface temperatures (SST) create optimal conditions for mangrove growth. Conversely, higher upwelling intensities, which are associated with cooler SSTs, are expected to contribute to more restricted mangrove distributions and reduced range limits.

2. Material and methods

2.1. Data

2.1.1. Upwelling presence and global map of upwelling intensity

The analysis focused on the relationship between upwelling intensities and mangrove areas. The continuous global map of upwelling intensity was obtained from the DataBasin product offered by The Nature Conservancy (accessible at https://databasin.org/) (Hoekstra et al., 2010). This map illustrates upwelling intensity data utilising Marine Provinces sensu Spalding et al. (2007) and classifies upwelling intensity into four tiers as delineated by Hoekstra et al. (2010): Level 1 (present), Level 2 (significant), Level 3 (important), and Level 4 (very important). Levels 1 and 2 signify low upwelling intensity, level 3 indicates intermediate intensity, and level 4 represents high intensity. Approximately 6.1 % (8556 km^2) of the total mangrove area mapped by Bunting et al. (2022) had no upwelling data and was excluded from the analysis. Because the upwelling map predominantly covers marine areas and some coastal mangroves fell outside its polygons, a 50 km buffer was generated around the upwelling map to ensure that all relevant mangrove polygons from the Global Mangrove Watch (GMW) map were accurately selected (more details in the GMW Section 2.1.2).

Data on well-developed upwelling systems were collected from multiple research sources (Appendix S1), and they were examined in relation to mangrove range limits. Previous studies, including Varela et al. (2015) and other authors, have identified and delineated coastal upwelling zones, as referenced in the literature (Appendix S1). These zones were marked with blue lines and include areas such as Benguela, Canary, Peru, Baja California, South Africa, Brazil, Somalia–Oman, India, China, southern Australia, and New Zealand. The relationship between the upwelling events and the mangrove distribution boundaries was assessed by delineating their corresponding influence zones (refer to Section 3 and Fig. 1).

2.1.2. Global mangrove map

The Global Mangrove Watch (GMW), initiated in 2011 as part of the JAXA Kyoto / Carbon Initiative, is a collaborative project led by Aberystwyth University and Solo Earth Observation, in partnership with Wetlands International, the International Water Management Institute, and the UN Environment World Conservation Monitoring Centre (U.K.) (Bunting et al., 2022). GMW has established a comprehensive global baseline map of mangroves for 2010. Additionally, it has monitored changes in mangrove coverage from 1996 to 2020 using satellite data from JERS-1 SAR, ALOS PALSAR, ALOS-2 PALSAR-2 and Landsat.

For this study, we utilised the Global Mangrove Watch Map Version 3 (Bunting et al., 2022) to determine the total mangrove area across different levels of upwelling intensity (see section 2.1.1). Despite its comprehensive coverage, the accuracy of mangrove range limits in global maps can be variable (Ximenes et al., 2023). To obtain precise geographical data on mangrove limits, we referred to the study by Quisthoudt et al. (2012), which provided validated global mangrove range limits through fieldwork, local expert surveys, and scientific literature. In this study, we define mangrove discontinuities as distinct breaks or gaps in the continuity of mangrove forest cover along coastlines. These discontinuities are characterised by the presence of mangroves in certain areas and their absence in others, despite seemingly suitable conditions. Potential factors influencing these gaps include temperature fluctuations, salinity changes, geographical barriers, and anthropogenic activities. Our objective is to assess whether upwelling systems contribute to these mangrove discontinuities.

2.2. Models and statistical analysis

Mangrove ecosystems were mapped using the Global Mangrove Watch Map (Version 3) at a 30 m resolution, processed in QGIS. Upwelling intensity values (Hoekstra et al., 2010) were assigned to each mangrove polygon. Records with invalid or missing values (e.g., zero, negative, or erroneous entries such as −9999) were removed, and only those polygons with upwelling intensity classified as 1, 2, 3, or 4 were retained. Because spatial scale may influence the detected relationship between upwelling and mangrove extent, the dataset was stratified into subsets based on different minimum area thresholds. Analyses were conducted for patches with areas ≥5 ha ($n = 85{,}665$), ≥50 ha ($n = 21{,}655$), ≥100 ha ($n = 13{,}926$), ≥200 ha ($n = 8602$) and ≥ 300 ha ($n = 6319$). These thresholds were selected to assess how local disturbances and edge effects in smaller patches might obscure broader environmental controls that become more evident in larger, contiguous mangrove stands. To mitigate issues related to data skewness, a logarithmic transformation was applied to the mangrove area (in hectares), generating the variable log_*area_hectares*. We used an Ordinary Least Squares (OLS) regression to figure out how the area of mangroves related to the strength of the upwelling in each subset. We specified the regression model as follows:

$$\begin{aligned}\text{area\_hectares} &= \beta_0 + \beta_1 \cdot \left(\text{upwell\_imp}, \text{Treatment}(4)\right) \\ &\quad + \beta_2 \cdot log(\text{area\_hectares}) + \varepsilon,\end{aligned}$$

where β_0 is the intercept, β_1 represents the coefficient for the categorical upwelling intensity levels (with class 4 as the reference), β_2 is the coefficient for the log-transformed mangrove area, and ε is the error term.

Variance Inflation Factors (VIFs) were computed to confirm that multicollinearity was low among predictors. Robust standard errors (with heteroscedasticity and autocorrelation consistent corrections using one lag) were applied in all regressions. All analyses were performed using Python (version 3.9). Diagnostic tests were also conducted to validate the assumptions of the OLS model. The distribution of residuals was inspected using histograms and kernel density estimates (KDE) to assess normality, and scatter plots of residuals versus fitted values were generated to identify patterns indicative of heteroscedasticity or autocorrelation. The Durbin-Watson statistic was computed to evaluate the presence of autocorrelation (with values near 2 indicating minimal autocorrelation), and the Anderson-Darling test was applied to assess residual normality.

Model fit was evaluated using the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and the coefficient of determination (R^2); these metrics, along with the regression summary, were used to determine the optimal model specification. Finally, visualisations (e.g., bar charts and other graphical representations) were employed to assess the distribution of mangrove areas across different upwelling intensity classes, thereby facilitating a comprehensive evaluation of spatial patterns.

3. Results

A global analysis reveals a significant spatial correlation between the distribution limits of mangroves and upwelling systems. Eight distinct mangrove range boundaries were found to coincide spatially with upwelling events. These locations include Baja California, Florida, Peru, southern Brazil, Angola, South Africa, southern China, and New Zealand. However, this pattern was not observed in regions such as western and southern Australia or southern Japan, where mangrove distributions do not align with upwelling systems (Fig. 1). Our analyses reveal a pronounced scale dependent relationship between upwelling intensity and mangrove area. When considering all mangrove patches ≥5 ha ($n = 85{,}665$), the OLS model yielded an R^2 of 0.203. In this dataset, upwelling class 1 reached only marginal significance, while the log transformed area variable was highly significant. This relatively low explanatory power suggests that the small, fragmented patches, which are subject to local disturbances and edge effects, may obscure broader environmental factors.

For patches ≥50 ha ($n = 21{,}655$), the model's explanatory power improved substantially, with the R^2 increasing to 0.370. In this subset, all upwelling categories became statistically significant, and the association between upwelling intensity and mangrove area was markedly strengthened. When the analysis was restricted to patches ≥100 ha ($n = 13{,}926$), the R^2 further increased to 0.432, reflecting even stronger associations between upwelling intensity and mangrove area. Subsequent increases in the minimum patch size threshold to ≥200 ha ($n = 8602$) and ≥ 300 ha ($n = 6319$) resulted in R^2 values of 0.497 and 0.537, respectively. In these larger, more contiguous systems, the statistical relationship between upwelling intensity and mangrove area became progressively more robust.

The three largest mangrove ecosystems, the Amazonian mangrove forest, the Sundarbans, and the mangroves of Northern Australia (Queensland and the Northern Territory), are located within these low-upwelling intensity areas (Figs. 2). As anticipated, regions with lower upwelling intensities have significantly more extensive mangrove forests. Specifically, 47.7 % of the global mangrove area is 66,763 km^2 (Fig. 3). This observation is particularly evident in the Indo-West Pacific (IWP) region, where upwelling intensity is generally lower than in major Eastern Boundary Upwelling Ecosystems (EBUEs).

Mangrove forests are scarce in regions with the highest upwelling intensity (level 4), which comprise only 1.9 % of the global mangrove area (2643 km^2) (Figs. 3). In the Gambia River and the Saloum Delta National Park in Senegal, there are around 2643 km^2 of mangrove areas within the highest levels of upwelling intensity (Figs. 2 and 3). The

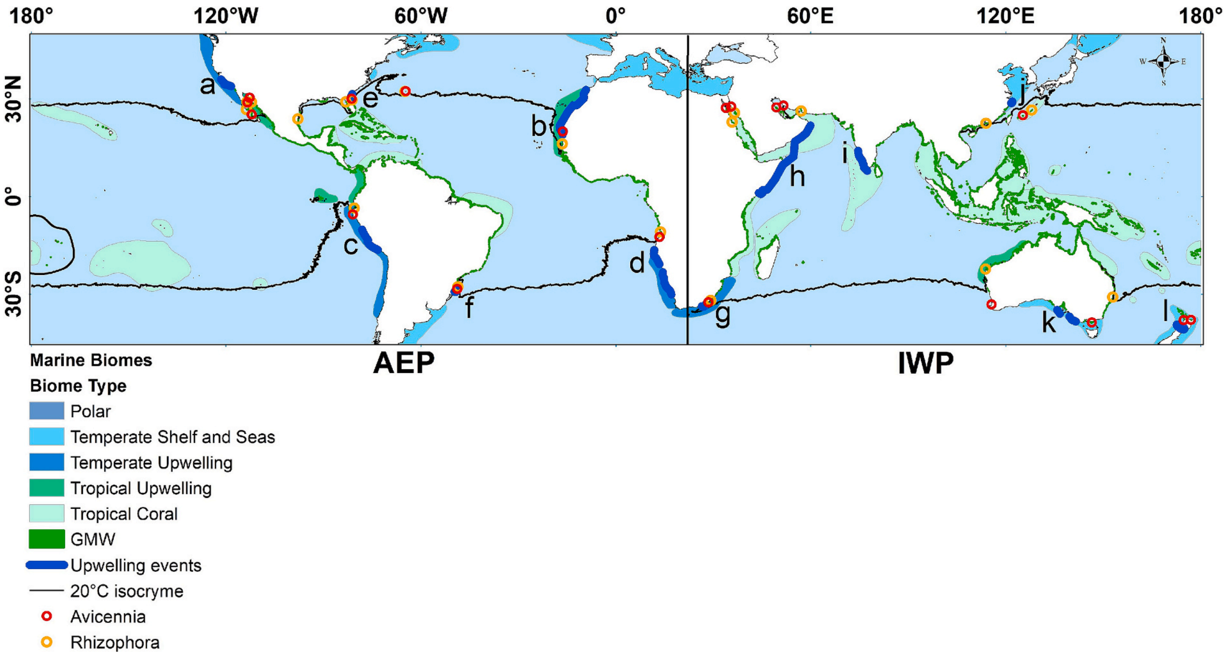

Fig. 1. The World Wildlife Fund Marine Biomes represents global marine ecoregions from the ESRI Data & Maps 2004 database (ESRI, 2004), there are five marine biome types. The Global Mangrove Watch (GMW) is represented in green along the coastline. The upwelling events (blue lines) show a rough representation of the upwelling zones predominant locations (see in section 2.1.1 and detailed georeferenced upwelling zones in Appendix S1). The East Boundary Currents (EBCs): (a) the California upwelling zone, (b) the Canary upwelling along the west coast of Africa with thin mangrove patches inside high upwelling intensity regions, (c) the Peruvian upwelling (related to the Humboldt Current) along the west coast of South America, and (d) the Benguela upwelling along the southwest coast of Africa with two main areas of influence of upwelling. The West Boundary Currents (WBCs): (e) the east coast of Florida, (f) the upwelling in Cabo de Santa Marta, (g) the Agulhas upwelling in South Africa, (h) the Somalia-Oman Complex upwelling and (j) the Yuedong upwelling in south China. Other minor upwellings also were found near to mangrove range limits: (i) upwelling along the west coast of India, coinciding with the Arabian upwelling zone, (k) the Bonney upwelling along the south coast of Australia, coinciding with the absence of mangroves, (l) the New Zealand upwelling. The black line represents the 20 °C isotherm of SST that was extracted from the Bio-Oracle database (Tyberghein et al., 2012) and generated in ArcGIS 10.3. The mangrove limits of the genus of Rhizophora and Avicennia mangrove species from Quisthoudt et al., 2012 data were put into the map, and the proximities with upwelling events were observed.

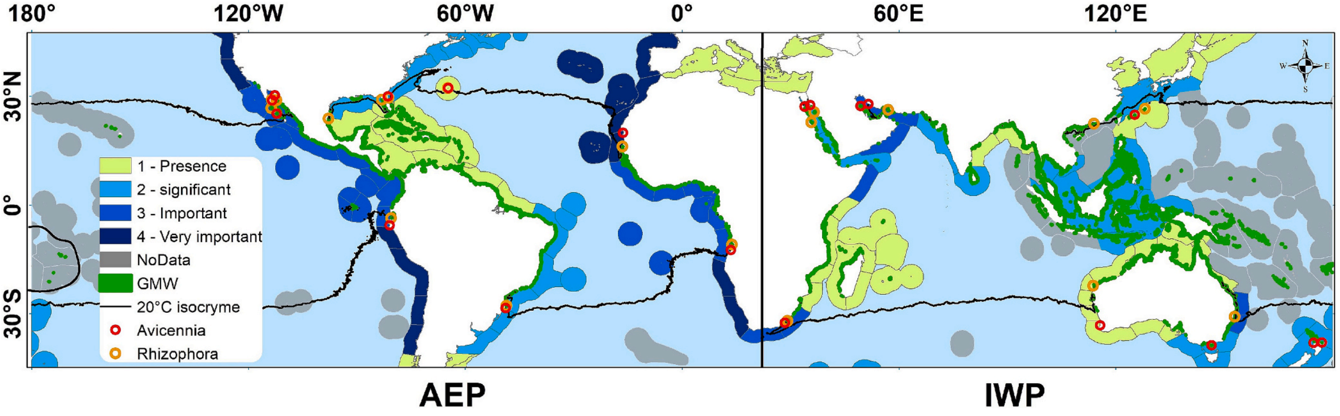

Fig. 2. The upwelling intensity map Hoekstra et al. (2010) displaying the four levels (see in section 2.1.1) for each marine province sensu Spalding et al. (2007). Mangroves are represented by dark green.

southern coast of South Africa, characterised by the Agulhas upwelling, represents a clear example of a mangrove range boundary (Fig. 2). Along the South African coast, mangroves are present to the north of Port Alfred but absent near Port Alfred and Port Elizabeth, where cold inshore waters associated with the Agulhas upwelling system limit mangrove growth (Lutjeharms et al., 2000) (Fig. 2). In New Zealand, the upwelling system near Kahurangi Point and Cape Farewell defines the southernmost boundary of mangrove distribution (Stanton, 1976; Bradford and Roberts, 1978; Shlrtcliffe et al., 1990; Vincent et al., 1991; Waters and Roy, 2004; Blanchette et al., 2009) (Fig. 2). On the southern shelves of Australia, the Bonney upwelling system in southern Australia, influenced by the relatively weak upwelling induced by the Leeuwin Current, contributes to the absence of mangroves along the coastline between Portland and Cape Jaffa (Rochford, 1977; Kämpf, 2015; McClatchie et al., 2006) (Fig. 2). These observations highlight the critical role of upwelling intensity in determining mangrove distribution limits along these coastal regions. The presence of this upwelling is likely a contributing factor to the absence of mangroves in these regions (Kämpf et al., 2004; McClatchie et al., 2006).

The Somalia-Oman upwelling system along the East African coast, from northern Somalia to Oman, is associated with a near absence of mangroves or the presence of only sparse populations dominated by a

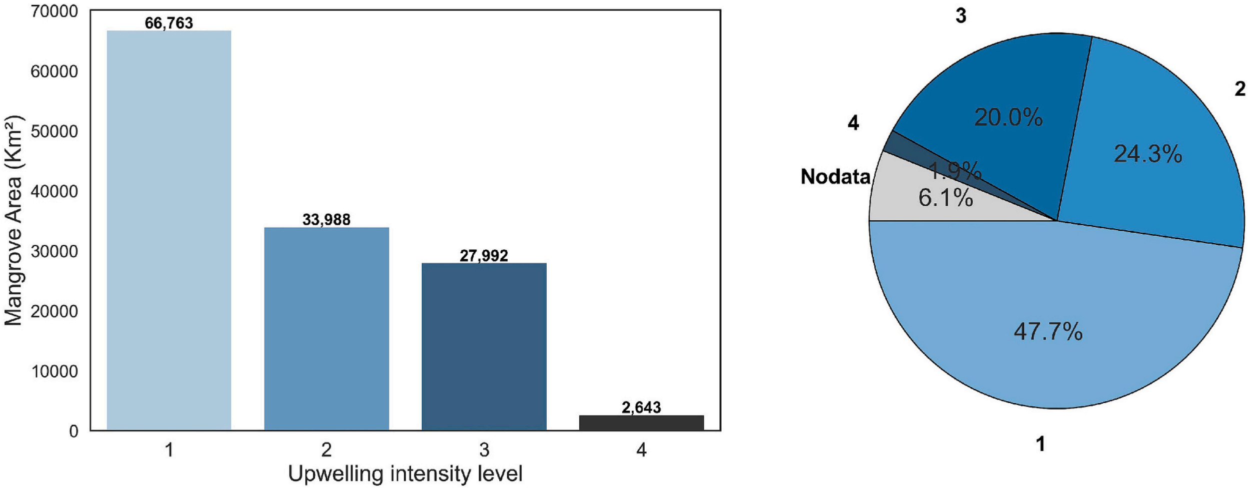

Fig. 3. The mangrove area (km^2) extracted from the Global Mangrove Watch map v.3 (Bunting et al., 2022) for each upwelling intensity level is as follows: (1) 66,763 km^2; (2) 33,988 km^2; (3) 27,992 km^2; (4) 2643 km^2. Additional details on upwelling intensity are found in Fig. 2 with intensity levels spatially distributed over the world. The percentage of mangrove area (km^2) extracted from the Global Mangrove Watch map v.3 for each upwelling intensity level is (1) 47.7 %; (2) 24.3 %; (3) 20 %; (4) 1.9 %. The NoData accounts for about 6.1 % of the mangrove area. The colours correspond to different upwelling intensity levels, with darker shades indicating higher intensities.

single species, *Avicennia marina* (Fig. 2) (Elliott and Savidge, 1990; Shi et al., 2000b; Izumo, 2008; deCastro et al., 2016). These zones exhibit a significant discontinuity in the otherwise continuous mangrove distributions along tropical coasts. Upwelling in the southeastern Arabian Sea, which influences the western coast of India between latitudes 8° and 14°N, appears to be linked to the limited presence of mangrove forests in this region, as shown in several global maps (Giri et al., 2011). Historically, mangroves were thought to extend only up to 18°N along the western coast of India (Fig. 2) (Smitha et al., 2014). This pattern of distribution is mostly due to the area's steep, vertical estuarine slopes and the lack of delta formation, which makes the intertidal zones too narrow for mangroves to grow (Kathiresan, 2018). However, recent updates to the Global Mangrove Watch v.3 database indicate that mangroves are now extending further north, beyond areas where upwelling intensity was previously thought to prevent their growth. Therefore, we need to conduct more ground-truth checks to ensure the accuracy of the updated mangrove distribution in areas with varying levels of upwelling.

Notably, sparse mangrove patches are observed in regions of high upwelling intensity. Within these zones of level 4, mangrove stands are limited to areas in Senegal and Gambia, situated near the boundary between levels 3 and 4. Mangroves in Mauritania were not mapped by the GMW map and are therefore not included in the highest upwelling category. Additionally, these mangroves are influenced by the Canary Upwelling, a prominent feature of the Eastern Boundary Upwelling Ecosystems (EBUEs) (Fig. 1 and Fig. 2).

4. Discussion

These findings strongly support our hypothesis that upwelling intensity exerts a scale-dependent influence on mangrove distribution. The relatively low R^2 observed for patches $\geq$5 ha indicates that when smaller and more fragmented mangrove patches are included, localised disturbances and edge effects may mask the broader environmental signal imparted by upwelling. Conversely, as the minimum area threshold increases, the models reveal both higher explanatory power and more robust, statistically significant effects of upwelling intensity. The enhanced model performance for larger mangrove stands ($\geq$50 ha, $\geq$100 ha, $\geq$200 ha, and $\geq$ 300 ha) suggests that environmental processes such as upwelling-driven cooling play a more determinative role in shaping extensive, contiguous mangrove ecosystems. In these systems, the impact of upwelling becomes increasingly pronounced, likely due to the reduced influence of localised factors. This interpretation is in line with previous studies that have highlighted the role of oceanographic processes in defining mangrove distribution limits. The most prominent upwelling systems that may act as barriers to the dispersal of mangrove propagules are in the EBCs in the AEP regions, where mangrove distributions are limited along the western coastlines of Africa and America. This pattern aligns with earlier observations in the literature (Chapman, 1975; Woodroffe and Grindrod, 1991; Lacerda and Schaeffer-Novelli, 1999; Lacerda, 2002).

Various studies have suggested that the northernmost mangrove limit on the southwestern coast of Africa is mainly driven by aridity rather than by temperature (Saenger, 2002). Apart from the western coasts of Australia and California, precipitation changes, rather than temperature, may be more influential in shaping mangrove limits in regions like Peru, Mauritania, and Namibia (Osland et al., 2017a). Consequently, aridity plays a key role in defining mangrove limits (Duke, 1992; Saenger, 2002; Quisthoudt et al., 2012; Osland et al., 2017a). According to Dupont et al. (2005), the Namibian upwelling (part of EBUEs) significantly contributes to coastal aridity. Upwelling systems, such as those off Peru, Baja California, the Canary Islands, and Namibia, create deserts like the Atacama (Peruvian upwelling), Sonoran (Californian upwelling), Sahara (Canary upwelling), and Namibia deserts (Benguela upwelling) (Shi et al., 2000a; Houston and Hartley, 2003; Adams, 2007). Intensified upwelling can exacerbate coastal aridity, affecting terrestrial vegetation (Shi et al., 2000a) and probably also mangrove ecosystems. An interesting observation, open for debate, is the lack of reported mangroves in Cabo Verde. This fact of mangroves along the Cabo Verde coastal areas is particularly intriguing because, in terms of geomorphology and climate zone, the archipelago appears to be suitable for mangrove colonisation (15°-17° N), even at low abundance, much as in Mauritania (Dahdouh-Guebas and Koedam, 2001). We suggested that the high-intensity upwelling events associated with the Canary upwelling system may be a significant factor limiting mangrove establishment in this region.

The equatorward West Australian Current is displaced offshore by the poleward-flowing Leeuwin Current, which transports warm waters from near-equatorial regions during winter (Smith et al., 1991; Pearce, 1991). Strong north–south thermohaline gradients between the Indonesian Throughflow and southwestern Australian waters are considered the primary force driving the Leeuwin Current (Batteen et al., 2007).

Importantly, this current suppresses the development of strong upwelling cells despite favourable wind conditions (Hanson et al., 2005; Varela et al., 2015). The warm waters carried by the Leeuwin Current significantly influence marine communities along the southwestern Australian coast (Morgan and Wells, 1991), creating a stark contrast with the western coasts of South America and Africa, where strong upwelling prevails. Although typical EBC regions exhibit pronounced upwelling, the presence of the Leeuwin Current renders the western coast of Australia an exception to these global patterns. Our analysis supports the view that the expansion of mangroves along the western Australian coast is closely linked to the suppression of strong upwelling. The anomalously warm coastal waters provided by the Leeuwin Current, as proposed by Semeniuk et al. (2000), likely enable mangroves to extend beyond 30°S in this region. In contrast with studies suggesting that restricted mangrove expansion is due to the influence of upwelling systems along the western coast of Australia (Chapman, 1975; Woodroffe and Grindrod, 1991).

In WBC regions, upwelling occurs at lower intensities than in EBC regions, making mangrove range limits less sensitive to upwelling and more responsive to factors such as cold air temperatures and reduced precipitation. For instance, in Japan the mangrove range (32°22′N) is associated with the warm waters of the Kuroshio Current, which creates favourable conditions for mangrove growth at higher latitudes (Woodroffe and Grindrod, 1991). Similarly, high-latitude mangrove limits are observed along the Gulf Stream on North America's eastern coast (Giri et al., 2011; Ward et al., 2016), the Brazil Current on South America's eastern coast (Soares et al., 2012), and the Agulhas Current off South Africa (32°36′S).The expansion of mangroves towards higher latitudes in the two major biogeographic regions (AEP and IWP) can be explained by the fact that the WBCs have much stronger, warmer, and faster currents than their eastern counterparts, the EBCs. Upwelling scenarios offer significant potential for advancing the understanding and management of mangrove ecosystems.

Future climate change projections suggest increases and decreases in upwelling intensity across various regions, potentially altering coastal winds and sea surface temperatures (SST) (Bakun, 1990; Sydeman et al., 2014; Varela et al., 2015; Wang et al., 2015). These changes could have considerable effects on mangrove distribution. Overall, the marked differences in model fit across spatial scales highlight the critical importance of considering scale in ecological assessments. By focusing on larger, more contiguous mangrove patches, where the influence of localised disturbances is minimised, our analysis provides a clearer understanding of how upwelling intensity and its associated climatic effects govern mangrove spatial extent.

Upwelling can be inferred from satellite data, mainly using sea surface temperature (SST) and wind datasets (Benazzouz et al., 2014), providing valuable information for future research aimed at correlating upwelling intensities with key mangrove structural and functional parameters such as biomass, tree height, productivity, and carbon storage. However, the absence of a comprehensive global upwelling index public available limits cross-regional studies and impedes direct comparisons. These insights are vital for refining global models of mangrove distribution and for informing conservation strategies under shifting oceanographic and climatic conditions. Moreover, while remote sensing offers a broad-scale perspective, the importance of ground-truth data and in-situ samples remains paramount. In addition, each mangrove species exhibits its own physiological threshold to environmental factors, underscoring the need for further laboratory studies encompassing diverse species to better understand the ecological niche and limits of each. This holistic approach will not only improve predictive models but also enhance conservation efforts in the face of ongoing climate change and evolving oceanographic dynamics.

5. Conclusion

This study demonstrates that upwelling systems play a critical role in shaping global mangrove distribution, with their influence being strongly scale-dependent. Our analyses reveal that while smaller mangrove patches (≥5 ha) exhibit limited and marginal responses to upwelling effects, larger contiguous mangrove systems (≥50 ha to ≥300 ha) show a progressively stronger relationship. These findings indicate that environmental processes associated with upwelling, such as cold-water-induced cooling and increased coastal aridity, are more apparent in extensive mangrove areas, where localised disturbances are minimised. These findings call attention to the importance of spatial scale in ecological assessments and provide critical insights for global-scale evaluations of mangrove dynamics. While previous research has acknowledged upwelling as a limiting factor for mangrove distribution, this study adds to the field by emphasising the complex interactions between upwelling and global mangrove distribution and area extent, a relationship previously underexplored.

The results highlight that upwelling significantly affects mangrove ecosystems by altering sea surface temperatures and creating climatic extremes that hinder mangrove growth. This effect is particularly evident in regions influenced by Eastern Boundary Currents, where high upwelling intensity correlates with sparse mangrove presence. In contrast, regions under the influence of warm Western Boundary Currents exhibit reduced upwelling, allowing mangroves to thrive at higher latitudes. Our findings indicate that the intensity and frequency of upwelling events significantly influence the response of mangrove ecosystems. Mangroves are notably absent from high-upwelling regions along the western coastlines of Africa and the Americas in the Atlantic East Pacific (AEP) biogeographic region. This absence is likely due to the unfavourable conditions generated by EBCs, which inhibit mangrove growth. In contrast, the Indo-West Pacific (IWP) region supports mangrove populations at higher latitudes, likely benefiting from reduced upwelling intensities associated with WBCs.

While marine currents do affect coastal ecosystems, it is the localised upwelling phenomena, influenced by specific geomorphological conditions, that play a more crucial role in shaping mangrove presence. Moderate upwelling intensity has been shown to impact essential phenological stages of mangrove species, including propagule production, which may limit the expansion of mangroves in regions with stronger upwelling. Consequently, large, uninterrupted mangrove expanses are typically found in areas with diminished upwelling intensity, where favourable environmental conditions, such as suitable geomorphology, support their development.

Our findings have important implications for global mangrove conservation and management. They suggest that accurate predictions of mangrove distribution and resilience require the incorporation of upwelling intensity as one more environmental variable. Moreover, these insights pave the way for future research into the complex interactions between oceanographic processes and coastal vegetation dynamics, particularly in the context of ongoing climate change. In summary, by elucidating the scale-dependent effects of upwelling on the mangrove area, this study provides critical insights into the biogeography of mangroves and highlights the need for integrated, multidisciplinary approaches to understand and conserve these vital ecosystems. These findings open new avenues for future research, offering new perspectives on how climate-related phenomena such as upwelling influence mangrove biodiversity and ecosystem services globally.

CRediT authorship contribution statement

Arimatéa C. Ximenes: Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Nico Koedam:** Supervision, Writing – review & editing. **Farid Dahdouh-Guebas:** Supervision, Conceptualization, Writing – review & editing. **Eduardo E. Maeda:** Writing – review & editing. **Leandro Ponsoni:** Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179356.

Data availability

All data is freely available

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