Salinity-induced limits to Mangrove canopy height and diversity

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Mangrove canopy height is a key metric to assess tidal forests’ resilience in the face of climate change. In terrestrial forests, tree height is primarily determined by water availability, plant hydraulic design, and disturbance regime. However, the role of water stress remains elusive in tidal environments, where saturated soils are prevalent, and salinity can substantially affect the soil water potential. Here, we use global observations of maximum canopy height, species richness, air temperature, and seawater salinity – a proxy of soil water salt concentration – to explain the causal link between salinity and Mangrove stature.

Our findings suggest that salt stress affects Mangrove height both directly, by reducing primary productivity and increasing the risk of xylem cavitation, and indirectly favoring more salt-tolerant species, narrowing the spectrum of viable traits, and reducing biodiversity. Yet, salt tolerance comes to a price. Highly salt-tolerant mangroves are less productive and generally shorter than more sensitive species, suggesting a causal nexus between salinity, biodiversity, and tree height. As sea-level rise enhances coastal salinization, failure to account for these effects can lead to incorrect estimates of future carbon stocks in Tropical coastal ecosys-
Canopy height is a critical variable in forest ecology. It regulates access to light, promotes diversity in plant functional types, and enhances ecosystem resilience to environmental disturbances (Walker et al., 1999; Falster and Westoby, 2003; Giardina et al., 2018; Detto et al., 2021). When interpreted through allometric relations, the height of trees also represents an essential parameter to estimate aboveground carbon stocks and design interventions to protect critically endangered ecosystems (Saenger and Snedaker, 1993; Moles et al., 2009; Worthington et al., 2020). In terrestrial forests, the height of trees is primarily controlled by water availability and biotic and abiotic factors, such as light competition, micro-climate, species allocation strategies, and the disturbance regime (Koch et al., 2004; Moles et al., 2009; Dybzinski et al., 2011; Klein et al., 2015; Tao et al., 2016; Giardina et al., 2018).

In contrast, in Mangrove forests thriving at the interface between the terrestrial and the marine environment, tidal inundation and river discharge maintain nearly saturated soil conditions, and physical water availability is far from being a limiting factor (Ball, 1988; Field et al., 1998). While alternative forms of water stress, like the limiting effects of pore water salinity on root water uptake and transpiration, could play a primary role in regulating Mangrove height, the broad mechanisms linking tidal drivers to canopy height remain largely unexplored.

Maximum canopy height, $H_{\text{max}}$, a parameter relatively easy to obtain from forest inventories, airborne LiDAR, or other remote sensing platforms (Lucas et al., 2002; Heumann, 2011; Fatoyinbo and Simard, 2013; Salum et al., 2020), has been extensively used to investigate the relation between Mangrove height and environmental drivers at the global scale (Friess, 2019; Simard et al., 2019b; Charrua et al., 2020). These studies have primarily focused on understanding how the latitudinal patterns of $H_{\text{max}}$ are affected by both fundamental climatic factors like precipitation and temperature and sporadic ecological disturbances such as tropical storms (Feher et al., 2017; Simard et al., 2019b; Charrua et al., 2020). Still, major tidal stress factors as soil pore water salinity display a large regional variability (Rovai et al., 2021) and can hardly be typified through zonal averages. Therefore, their effects remain more challenging to pinpoint in global studies.

Salinity has been long-known as one of the dominant sources of abiotic stress in coastal wetlands, regulating local carbon allocation and production (Ball, 1988; Alongi, 1998; Perri et al., 2019). Gradients of salinity have been linked to tidal zonation, species succession and abundance at the ecosystem scale (Greiner La Peyre et al., 2001; Wendelberger and Richards, 2017; Perri et al., 2018b). Moderate salinity is generally associated with high species richness (Ball, 1998; Islam et al., 2016), which has been related to elevated productivity (Mittelbach et al., 2001; Bai et al., 2021). While the relationship between species diversity and productivity remains controversial and may depend on the spatial scale of interest (Whittaker and Heegaard, 2003; Mensah et al., 2018), biotic interactions (e.g., competition for light or ecological facilitation) promote tall canopies in highly diverse Mangrove forests (Wolf et al., 2012; Meyer et al., 2020). Affecting species richness, salinity may, therefore, exert an indirect control on canopy height.

At the same time, salinity is a primary hydrological driver, known to reduce soil water potential, limit root water uptake, increase the risk of xylem cavitation, and impair photosynthesis (Munns, 2002; Perri et al., 2018a, 2019, 2022). Recent studies on Mangrove biomass stocks and allometric relations have suggested that aridity and tidal
FIGURE 1  Hydrologically-driven versus salinity-driven hydraulic stress. Conceptual representation of water stress in terrestrial (A) and tidal (B) forests, as regulated by the total soil water potential $\psi_{\text{tot}}$, defined as the sum of matric potential $\psi_s$, osmotic potential $\psi_\pi$, and gravimetric potential $\psi_h$. In terrestrial forests (A), water movements in the soil are mainly controlled by $\psi_s$ and soil moisture patterns (hydrologically-driven hydraulic stress). In contrast, in tidal environments (B), soils are primarily saturated ($\psi_s \approx 0$), and the contribution of $\psi_\pi$ becomes dominant (salinity-driven hydraulic stress).

Inundation frequency – which are both strongly correlated with water salinity – are dominant limiting factors for coastal ecosystems’ carbon storage [Adame et al. 2020; Bathmann et al. 2021; Rovai et al. 2021]. These effects are analogous to those of water stress in terrestrial forests, and similarly to water stress, they could exert significant controls on species competition and canopy height [Koch et al. 2004; Klein et al. 2015]. While in terrestrial forests the soil water potential, $\psi_{\text{tot}}$, is governed by soil moisture availability (hydrologically-driven hydraulic stress; Figure 1A), in saturated tidal soils the matric potential, $\psi_s$, is close to zero, and osmotic effects largely regulate access to water (salinity-driven hydraulic stress; Figure 1B). Accordingly, salinity should be regarded as a form of tidal aridity, capable of imposing major constraints to Mangrove canopy dynamics and productivity.

Here we investigate the relation between pore water salinity and Mangrove height across scales ranging from regional to global. Our main hypothesis is that the interplay of salt stress and plant salt tolerance can be used to explain and generalize this relation across a large variety of coastal ecosystems worldwide – in analogy with the effects of water stress in terrestrial ecosystems. We also hint at the causal relation between salt-stress, species succession, and species richness as one of the primary mechanisms through which salinity can affect Mangrove height at regional and global scales.
2 | DATA AND METHODS

2.1 | Data Sources

Our analysis relies on the global Mangrove maximum canopy height ($H_{\text{max}}$) dataset generated by Simard et al. (2019a) by integrating the Shuttle Radar Topography Mission (SRTM) digital elevation model (Farr et al., 2007) with the LiDAR heights from the Geoscience Laser Altimeter System (GLAS) mission (Fatoyinbo et al., 2008). The dataset, which also provides global estimates of Mangrove distribution and aboveground biomass, is made publicly available from the Oak Ridge National Data Archive (ORNL DAAC) at a native 30-meter spatial resolution. Both SRTM and GLAS retrieval refers to the year 2000. To limit Mangroves’ misattribution away from coastal areas, we masked the raw Mangrove canopy height data with the spatial distribution of Mangroves reported in the World Atlas of Mangroves (Spalding, 2010).

The World Atlas of Mangroves was also used to infer global patterns of species richness, $SR$, by overlaying the spatial coverage at 30 meters resolution of the 60 Mangroves species listed in the Atlas. $SR$ is estimated as the number of species with the same bio-geographical distribution, and represents a potential $SR$. The actual number of species per plot is expected to be lower, as fast-growing (and potentially taller) species out-compete the less productive ones.

Maximum canopy height was investigated as a function of historical mean air temperature ($T_{\text{air}}$; representing here climatic forcing) and sea-surface salinity ($S_{\text{sw}}$). While other environmental variables such as precipitation and evapotranspiration are expected to be correlated with pore water salinity (Kelble et al., 2007; Rovai et al., 2021), the salt mass balance of a Mangrove ecosystem depends not only on these local environmental conditions but also on large-scale ocean circulation and the quantity and quality of riverine inputs (Lane et al., 2007; Gomez et al., 2019). Given such complexity and the lack of direct measurements of soil salinity, $S_{\text{sw}}$ represents the best available proxy for salinity in coastal ecosystems and was, therefore, selected for the analysis performed here. Air temperature, $T_{\text{air}}$ across the Mangrove biogeographical range ($39^\circ \text{S} - 30^\circ \text{N}$) was obtained from the WorldClim dataset (Fick and Hijmans, 2017) over the period 1970–2000, while sea-surface salinity, $S_{\text{sw}}$ was derived from the GLORYS12V1 reanalysis (Bourdalle, 2012) for the years 1993-2018. WorldClim and GLORYS12V1 products are provided as monthly averages at a 30 arc-seconds and 300 arc-seconds spatial native spatial resolution, respectively. Although $S_{\text{sw}}$ and $T_{\text{air}}$ time spans are not completely overlapping, their temporal extent is sufficient to derive long-term means that can be used as explanatory variables for $H_{\text{max}}$. All the data were aggregated at 10-minutes spatial resolution (600 arc-seconds, about 18.5 km at the equator), and average values were obtained for each pixel.

Mangrove canopy height was associated with mean salinity and air temperature based on a proximity analysis. This was obtained through the use of a focal statistic where, for each $H_{\text{max}}$ pixel, the corresponding $S_{\text{sw}}$ and $T_{\text{air}}$ were calculated as average values among neighboring cells (up to 5×5 cells).

2.2 | Latitude-dependent and Site-dependent analyses

The relation between mangrove canopy height, salinity, air temperature and species richness was explored both zonally (latitude-dependent analysis) and locally (site-dependent analysis). In the latitude-dependent analysis, each variable was then averaged zonally over 1° of latitude, reducing the sample size to 70 averages corresponding to the observed geographical range of Mangrove ecosystems ($39^\circ \text{S} - 30^\circ \text{N}$). The zonal averages where calculated at the global scale and across the different bio-geographic regions: (a) Americas and West Africa (AWA: $120^\circ \text{W} - 13^\circ \text{E}$), (b) East Africa and Middle East (EAME: $30^\circ \text{E} - 77^\circ \text{E}$), and (c) Indo-Pacific Asia (IPA: $78^\circ \text{E} - 152^\circ \text{W}$; Figure 1E-G). The site-dependent analysis, in contrast, was performed comparing the local gridded $H_{\text{max}}$, $S_{\text{sw}}$, and $T_{\text{air}}$ data to $SR$ estimates.
We explored how the main statistical descriptors (i.e., median, 25th and 75th percentiles, min and max non-outlier values) of $H_{\text{max}}$, $S_{\text{sw}}$, and $T_{\text{air}}$ vary as a function of $SR$.

Finally, to reduce the variability of $H_{\text{max}}$ within the dataset and partially decouple the direct impact of salinity on canopy height from the indirect effect mediated by species richness, the relation between canopy height and environmental variables was investigated analyzing the mean values of $H_{\text{max}}$ as a function of mean $S_{\text{sw}}$, and $T_{\text{air}}$, conditional to species richness ($\langle H_{\text{max}} | SR \rangle$). The $\langle H_{\text{max}} | SR \rangle$ was also related to the $S_{\text{sw}}$ coefficient of variation, $CV_{S_{\text{sw}}}$, and a modified $CV$ for air temperature, $CV_{T_{\text{air}}}^{*}$. The latter was calculated with respect to the optimal temperature value $T_{\text{opt}}$, identified around the mode of the global $T_{\text{air}}$ distribution in Mangrove ecosystems ($\sim 27^\circ\text{C}$; see Section 3.2). We first computed the mean deviation ($\sigma_{T}^{*}$) around $T_{\text{opt}}$. The modified coefficient of variation was then estimated as $CV_{T_{\text{air}}}^{*} = \sigma_{T}^{*} / T_{\text{opt}}$, which reflects the seasonal variability of the mean air temperature around its optimal value.

2.3 | Analysis of variance

Previous studies have quantified the impact of $T_{\text{air}}$, $S_{\text{sw}}$ and precipitation on Mangroves biomass stocks by performing ordinary least squares regression (OLSR) analyses (Rovai et al., 2018; Ribeiro et al., 2019; Simard et al., 2019b). However, OLSRs can yield ambiguous results in case of high multicollinearity (Naes and Martens, 1985) that is expected, for example, between $T_{\text{air}}$ and $SR$. Here, the significance of the relations between $H_{\text{max}}$ and the selected environmental drivers ($S_{\text{sw}}$, $T_{\text{air}}$, and $SR$) was tested through multivariate regression analysis. We opted for a partial least-squares regression (PLSR) model, which has the advantage of accounting for the possible multicollinearity among the predictor variables (Rosipal and Krämer, 2005).

The selection of environmental variables to include in the PLSR model was based on the results of previous studies (Simard et al., 2019b; Rovai et al., 2021) and on the observation that rainfall, tidal regime, and evapotranspiration, rather than directly affecting mangroves productivity, are all proxies of salinity (Fosberg, 1961; Field, 1995). Simard et al. (2019b), in particular, considered a wide range of bioclimatic variables and concluded that the latitudinal variation of maximum canopy height can be explained by just average temperature and average annual precipitation. Species richness was not included in their regression model. Rovai et al. (2021) suggested that Mangrove biomass stocks are controlled by local or regional forcings rather than latitude-dependent averages. They found that aridity, tidal amplitude, and duration, all proxies of salinity, explain most of the $H_{\text{max}}$ variance when analyzed at the ecosystem (local or pixel) scale. Based on these previous findings, and to test our hypothesis that both salinity species richness could affect Mangrove canopy height, we selected $S_{\text{sw}}$, $T_{\text{air}}$, and $SR$ as plausible explanatory variables for both the latitude-dependent and site-dependent analyses.

The PLSR, performed running the SIMPLS algorithm (De Jong, 1993), was used to explain the observed variance in both the latitude- and site-dependent patterns. We first used a univariate regression model to estimate the variance explained by each variable alone. We then combined the three variables through the multivariate PLSR. The best PLSR models (i.e., the ones that can explain most of the variance) were obtained by including all the variables in the latitudinal analysis. We excluded $T_{\text{air}}$ from the site-specific model because of its high correlation with $SR$ (see Section 3.3).
3 | RESULTS AND DISCUSSION

3.1 | Regional versus global salinity controls on Mangrove canopy height

In line with previous studies performed in terrestrial forests, many authors have focused on the relation between Mangrove height – as a proxy of above-ground biomass – and major climatic drivers, such as precipitation and air temperature (Pickens and Hester, 2011; Friess, 2019; Simard et al., 2019b; Charrua et al., 2020). These studies consistently show that the latitudinal variability of Mangrove height strongly correlates with air temperature and precipitation, concluding that these climatic factors alone can explain most of the observed spatial variability of $H_{max}$.

However, the analysis of global correlations is only one part of the tale. Rather than directly affecting canopy height, air temperature and precipitation might shape the latitudinal patterns of $H_{max}$ indirectly through their control on aridity and species richness. There is a broad scientific consensus around the idea that the ecological role of air temperature is to determine the geographical range of Mangrove ecosystems, thus affecting biodiversity rather than directly influencing canopy height (Clough et al., 1982; Duke et al., 1998; Osland et al., 2016). Besides, temperature governs evapotranspiration, which with precipitation regulates the concentration of salts in the soil pore water and, more broadly, aridity (Osland et al., 2016; Rivera-Monroy et al., 2017).

In the same way, it is unlikely that freshwater inputs from precipitation can significantly influence soil water availability and plant status in tidal areas, where soils are predominantly saturated (Ball, 1988; Field et al., 1998). Although precipitation is related to river discharge and nutrient delivery (Twilley and Day, 1999; Reef et al., 2010), its primary role in coastal wetlands is to dilute soil water salinity (Fosberg, 1961; Rodriguez et al., 2016). As a result, it should be regarded as a proxy for salinity rather than a climatic factor affecting $H_{max}$ directly (Fosberg, 1961; Field, 1995; Gilman et al., 2008).

At the same time, salinity controls on tidal ecosystems are local in nature, making it challenging to establish a clear nexus between salt stress and canopy height at the global scale (Ward et al., 2006). Contrary to climatic drivers like average air temperature, which displays distinct latitudinal patterns in response to irradiance distribution (Figure 2A), coastal seawater salinity can be affected by the local hydrological regime, coastal geomorphology, tidal controls and thermohaline circulation (Schmidt et al., 2004; Schmitt, 2008; Herbert et al., 2015) (Figure 2B). In addition, while mangroves are halophytes, their adaptations to salinity vary widely across the different species, resulting in a broad spectrum of physiological responses to salt stress (Parida and Jha, 2010; Reef and Lovelock, 2015).

To pinpoint these local effects, we disaggregated global patterns of maximum Mangrove height ($H_{max}$), sea surface salinity ($S_{sw}$; a proxy for pore water salinity in coastal ecosystems), mean air temperature ($T_{air}$; representing climatic forcing), and species richness ($SR$) to the regional scale (see Methods). Although consistent with previously observed latitudinal patterns, our latitude-dependent analysis suggests that $SR$ is the primary covariate of the observed $H_{max}$ distribution, with $S_{sw}$ and $T_{air}$ only weakly correlated to canopy height (Figure 2D-G). Due to its inhomogeneous latitudinal distribution, salinity appears to be a poor descriptor of $H_{max}$ when analyzed at the global scale (Figure 2D). However, it shows different – and at times marked – regional impacts on the AWA, EAME, and IPA Mangroves (Figure 2F-E). In the AWA region (Figure 2E), characterized by a wide range of salinity conditions and intermediate biodiversity, $S_{sw}$ appears to exert a clear influence on $H_{max}$. In contrast, this relation is more elusive in the EAME region (Figure 2F) – characterized by extreme salinity conditions and meagre to intermediate biodiversity – and in the IPA Mangroves (Figure 2G), where low to moderate salinity conditions and high biodiversity represent the norm. These results might suggest that the influence of $S_{sw}$ on $H_{max}$ is, to some extent, mediated by species richness.
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Figure 2: Global versus regional drivers of Mangrove canopy height: Global multi-year average of A) mean air temperature ($T_{\text{air}}$) from the WorldClim dataset (Fick and Hijmans, 2017) for the period 1970-2000, and B) surface seawater salinity ($S_{\text{sw}}$) from the GLORYS12V1 reanalysis over the period 1993-2018 (Bourdalle, 2012). Data are shown for the latitude range $39^\circ$S – $30^\circ$N, which spans the entire Mangrove biogeographical range as reported in the World Mangrove Atlas (Spalding, 2010). The dashed rectangle in B) highlights areas of high regional salinity variability. C) Global distribution Mangroves species richness ($SR$) derived from the World Mangrove Atlas (Spalding, 2010). D-G) Latitudinal distribution of $H_{\text{max}}$ (green lines), $T_{\text{air}}$ (red lines), $S_{\text{sw}}$ (light blue lines), and $SR$ (black lines) at a global scale, E) in the AWA, F) EAME, and G) IPA regions. The blue shaded area in F) indicates a range of EAME latitudes where data are too scarce to support the analysis.

3.2 | Biodiversity-mediated salinity controls

To better investigate the role of biodiversity in regulating Mangrove canopy height, we explore the regional dependence of $H_{\text{max}}$, $S_{\text{sw}}$, and $T_{\text{air}}$ from $SR$. Consistently with results from terrestrial forests (Gatti et al., 2017; Marks et al., 2016), $H_{\text{max}}$ shows a distinct dependence on species richness, sharply increasing with biodiversity (Figure 3A-C). Low diversity, in contrast, is associated with short canopies. Although the complexity of coastal ecosystems and the high number of confounding factors hinder our capability to disentangle some cause-effect relations, these findings seem
FIGURE 3  Structure of the empirical relations between canopy height, air temperature, salinity, and species richness: Box plots of (A-C) maximum Mangroves canopy height [m], (D-E) salinity [psu], and (G-I) air temperature [°C] or given species richness, SR, in the three considered sub-regions (AWA, EAME, and IPA). Red central marks indicate the median, and the bottom and top edges of the boxes indicate the 25th and 75th percentiles, respectively. The whiskers extend to twice the interquartile range, and the more extreme points are considered outliers (not shown). The optimal air temperature value corresponds to $T_{\text{air}} = 27^\circ \text{C}$ circa. 

The analysis of the $T_{\text{air}}$–SR (Figure 3D-F) and $S_{\text{sw}}$–SR (Figure 3G-I) relations, at the same time, indicates that both $T_{\text{air}}$ and $S_{\text{sw}}$ are major abiotic co-factors in controlling species richness. While elevated salt-stress and low temperature are generally coupled with low species richness, high diversity is attained in ecosystems with moderate $S_{\text{sw}}$ and elevated $T_{\text{air}}$, such as in the IPA Mangroves. While air temperature is often the dominant constraint for species diversity to support the hypothesis that high species diversity can promote competition for light and resources, resulting in taller Mangrove trees [MacArthur and Wilson 1967; Gatti et al. 2017].

Additionally, in ecotones characterized by low salinity, tall forests create opportunities for short shade-tolerant species to coexist with tall and light-demanding Mangroves [Lugo 1986]. It is also likely that the conditions that lead to high species richness promote high productivity and taller canopies [Lovelock 2008; North et al. 2017]. Moderate salinity typical of intertidal estuarine ecotones, for example, may result in both high productivity and elevated species richness [Spalding 2010; Simard et al. 2019b; Friess 2019]. To better unravel the direct effect of salinity on canopy height from the indirect effect due to species richness, we also analyzed the average $H_{\text{max}}$ for given SR (see Section 3.3 and Figure 4).
To assess the relative impact of $T_{\text{air}}$ on $S_{\text{sw}}$ and $H_{\text{opt}}$, the emergences of this optimal value results from a) the reduction in light-saturated photosynthetic rates, stomatal conductance, and photosynthetic efficiency, known to occur in Mangroves at $T_{\text{air}} < T_{\text{opt}}$ (Davis, 1940; Ball, 1988; Saenger, 2002; Kao et al., 2004; Barr et al., 2009), and b) heat stress at $T_{\text{air}} > T_{\text{opt}}$ to which Mangroves adapt producing energetically-costly osmolytes such as proline (Liu and Wang, 2020). Ultimately, both extremely high and low temperatures reduce the biogeographical range of Mangroves, with very few species surviving in temperate or hot environments (Spalding, 2010; Alongi, 2012).

Whether elevated temperatures represent an additional source of stress and an ecological constraint for EAME $H_{\text{opt}}$ (Medina, 1999; Zahed et al., 2010), salinity seems to be a dominant stress factor. Temperatures around an optimal value, $T_{\text{opt}}$, corresponding to about 27°C, in the IPA region harbour the highest richness (Duke et al., 1998). The emergence of this optimal value results from a) the reduction in light-saturated photosynthetic rates, stomatal conductance, and photosynthetic efficiency, known to occur in Mangroves at $T_{\text{air}} < T_{\text{opt}}$ (Davis, 1940; Ball, 1988; Saenger, 2002; Kao et al., 2004; Barr et al., 2009); and b) heat stress at $T_{\text{air}} > T_{\text{opt}}$ to which Mangroves adapt producing energetically-costly osmolytes such as proline (Liu and Wang, 2020). Ultimately, both extremely high and low temperatures reduce the biogeographical range of Mangroves, with very few species surviving in temperate or hot environments (Spalding, 2010; Alongi, 2012).

3.3 Quantifying the impact of climatic and ecological forcing on $H_{\text{opt}}$

To assess the relative impact of $T_{\text{air}}$, $S_{\text{sw}}$, and $SR$ on Mangrove canopy height, the couplings observed across latitudes and at the local scales (Figures 2D-G and 3) were tested a) using a multivariate partial least-squares regression (PLSR; Tables 1 and 2). For the IPA region, the percentage of variance explained by the predictor variables, accounting for possible multicollinearity (Chong and Jun, 2005). The analysis revealed that $SR$ is the main controlling factor for $H_{\text{opt}}$ in the latitude-dependent framework, explaining alone up to about 80% of the global variability (Table 1). The percentage of variance explained by $SR$ at the regional level is significantly lower (41.8%–57.4%) than the global one, suggesting that specific climatic factors become more important at the local scales. We find that, if partial correlations are taken into account, $H_{\text{opt}}$ is only weakly related to $H_{\text{opt}}$, and it does not significantly improve the performance of the regression model. These results suggest that the previously-reported impact of $T_{\text{air}}$ on Mangrove canopy height (Woodroffe and Grindrod, 1991; Duke et al., 1998; Spalding, 2010; Osland et al., 2017; Simard et al., 2019b) may be attributed to the temperature-dependent geographical distribution of $SR$.

Salinity is shown to be a crucial driver at the ecosystem scale controlling $H_{\text{opt}}$ both directly, as a source of environmental stress, and indirectly, by limiting biodiversity. Although $SR$ remains the most correlated variable also in the site-specific analysis explaining up to 34% of the variance in $H_{\text{opt}}$, $S_{\text{sw}}$ becomes a significant predictor that explains up to 26% of the spatial variability (Table 2). The relation between $H_{\text{opt}}$ and $S_{\text{sw}}$ shown in Figure 3A further supports the hypothesis that salinity can exert significant controls on canopy height. On average, Mangrove height decreases with salinity following a power law ($R^2 = 0.52$). In turn, the variability of $S_{\text{sw}}$, quantified through its coefficient of variation $CV_{\text{sw}}$ (see Methods), is not directly related to $H_{\text{opt}}$ (Figure 4B), and displays a ‘threshold behavior’ similar to the control shown by mean temperature (Figure 4C). Protracted and spatially homogeneous
freshwater or hypersaline conditions result in low species richness (Ball, 1998). Yet, ecosystems with relatively low SR (smaller dots in Figure 4A) can attain elevated heights if salt concentration is low, as a consequence of the coexistence of a moderate number of highly productive species. Variability in salinity and mean air temperature seem to impose ecological thresholds that determine biodiversity and only indirectly affect biomass stocks. This threshold can be easily identified for $T_{\text{air}}$ around the optimal value $T_{\text{opt}}$.

Interestingly, our results show that $\langle H_{\text{max}} \mid SR \rangle$ decreases as a function of the modified temperature coefficient of variation $CV_{T_{\text{air}}}^*$, calculated as the ratio between the mean deviation around $T_{\text{opt}}$ and the average air temperature (Figure 4D). Low $CV_{T_{\text{air}}}^*$ thus indicates minimal temperature fluctuations around the optimal value. This finding is in agreement with previous studies, including Cavanaugh et al. (2019), who observed an expansion of Mangrove ecosystems in the Florida Everglades as a consequence of the reduction in temperature fluctuations and freezing events.
TABLE 1  PLSR results, latitudinal analysis. All values are averaged zonally over 1° of latitude across the globe, and for the AWA (120° W - 13° E), EAME (30° E - 77° E), and IPA (78° E - 152° W) region. The table displays the percentage of variance explained by the regression models at the global scale and for the different regions.

| Predictor       | Global | AWA       | EAME      | IPA       |
|-----------------|--------|-----------|-----------|-----------|
| $SR$ alone      | 80.4%  | 57.4%     | 41.8%     | 51.7%     |
| $S_{sw}$ alone  | 40.5%  | 51.7%     | 25.2%     | 0.2%      |
| $T_{air}$ alone | 35%    | 28.7%     | 7.1%      | 28.6%     |
| **Total**       | 85%    | 74.6%     | 42.8%     | 61.4%     |
| $SR, S_{sw}, T_{air}$ | (79.1,4.6,1.2) | (62.4,7.0,5.2) | (38.2,4.3,0.3) | (50.5,2.2,8.6) |

TABLE 2  PLSR results, site-specific analysis. All variables refer to the local (pixel) scale. Being highly correlated with species richness, $T_{air}$ is not included in the multivariate analysis.

| Predictor       | AWA       | EAME      | IPA       |
|-----------------|-----------|-----------|-----------|
| $SR$ alone      | 33.8%     | 30.4%     | 16.4%     |
| $S_{sw}$ alone  | 26%       | 6.7%      | 0.35%     |
| $T_{air}$ alone | 4.1%      | 7.1%      | 4.4%      |
| **Total**       | 59.8%     | 37.1%     | 16.8%     |
| $SR, S_{sw}$    | (33.8,26.0) | (30.4,6.7) | (16.4,0.3) |

4  | CONCLUSION

We hypothesize that the salinity-induced limitation of canopy height results from a combination of different underlying processes, which can be summarized as follows. Analogously to water stress, salinity reduces soil water potential because of osmotic effects [Munns, 2002; Perri et al., 2017, 2018a]. As canopy height increases, the osmotic stress intensifies the plant effort to sustain a leaf water potential that becomes more and more negative [Koch et al., 2004; Klein et al., 2015]. As a result, salinity may impose a species-specific upper limit on canopy height, and Mangrove ecosystems experiencing prolonged and severe salt stress may tend to maintain a short canopy to avoid xylem cavitation [Lovelock et al., 2006; Rossi et al., 2020].

Similarly, salinity limits carbon assimilation and biomass production [Munns and Tester, 2008; Perri et al., 2019]. Salt-stressed plants prefer to allocate carbon in the root system at the expense of canopy expansion to maximize water use efficiency [Clough et al., 1982; Barr et al., 2013]. Although the below-ground biomass of these ecosystems can become a significant carbon pool, above-ground carbon stocks and height are significantly limited [Komiyama et al., 2008]. We further argue that severe stress induced by salinity reduces the niche breadth by excluding less tolerant species and decreases competition for above-ground resources, limiting diversity and $H_{max}$ [Ball, 1998]. Contrarily, more tolerable salinity conditions might boost competition for light, enhance forest structural complexity and frequency.
promote species coexistence, thus increasing canopy height and Mangrove productivity through complementary re-
source utilization (Tilman et al., 2012; Grace et al., 2016). The observed high $H_{\text{max}}$ attained by tropical Mangrove 
ecosystems is, therefore, the outcome of the evolutionary competition for light and above-ground resources under 
favorable environmental conditions.

Given the sharp gradients of salt concentration in coastal environments, salinity-induced limitations of $H_{\text{max}}$ can 
have significant ecological implications under projected climate change and sea-level rise. A small increment in the 
sea level can lead to large sea-water intrusions (Werner and Simmons, 2009), sizable soil salinisation (Fagherazzi et al., 
2019), and may reduce biodiversity and biomass stocks (Hayes et al., 2019; Bai et al., 2021). Failure in accounting for 
salinity impacts and salinisation-induced ecosystems shifts may lead to inaccurate predictions of Mangrove carbon 
stocks and species diversity, impairing our ability to design appropriate conservation measures to protect these vital 
ecosystems.

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Conflict of interest

The authors declare that they have no competing financial interests.

Data availability

Mangrove canopy data were made available by the Oak Ridge National Data Archive (ORNL DAAC). Sea surface salinity 
data in proximity of coastlines were obtained from the GLORYS12V1 reanalysis product, while the air temperature 
data were extracted from the WorldClim global dataset. The global distribution of Mangrove species (60 species) was 
made available by the authors of the World Atlas of Mangroves (Spalding, 2010).

Author contributions

S.P. and A.M. designed and performed research; S.P. analyzed data; M.D. and A.P. helped design the testing hypothesis 
and develop the statistical analysis; S.P. and A.M. wrote the paper with inputs from all the authors.

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