ORIGINAL PAPER

# Temperature variation among mangrove latitudinal range limits worldwide

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**Abstract** Mangroves are mainly tropical tree species that occur on either side of the equator and because temperature decreases with increasing latitude, the latitudinal limits of mangroves are expected to be mainly controlled by temperature-related drivers. Here, we hypothesized that the mangrove genera (*Avicennia* and *Rhizophora*) have the same limiting temperature at all of their upper latitudinal limits at the global scale. We first derived six parameters from monthly mean sea surface temperature (SST) and air temperature (AT). Furthermore, we investigated whether the variation in these temperature parameters is related (i) to the position of the limit, (ii) to specific temperature requirements of congeneric species and/or (iii) to aridity.

Communicated by C. Lovelock.

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All temperature-based parameters derived from AT and SST are highly variable among the upper latitudinal limits of *Avicennia* and *Rhizophora*. Hence, we found no common isotherms to characterize the limits of the two mangrove genera, which contradict previous studies. The high temperature variation among limits can be due to partial range filling towards the latitudinal limits. This is supported by the higher warmest month temperatures at the latitudinal limits of the northern hemisphere as compared to the southern hemisphere. However, temperature parameters at limits, with no or less than 250 km of available poleward coast, are not different from other limits, and adult tree height at the limits is not correlated with the temperature-based variables. Mean air temperature is warmer at limits with an arid climate, suggesting mechanisms of compensation towards higher temperatures when *Avicennia* and *Rhizophora* have to cope with both aridity and low temperature.

## Introduction

A range limit is a theoretical line between the areas in which a particular species/ecosystem does and does not occur. In nature, range limits are transition zones with several possible intermediates (Körner and Paulsen 2004). Most tree species show specific latitudinal range limits at their upper latitudinal edges. This has long attracted biogeographers and suggests a temperature-related explanation. If such temperature-based drivers can be identified accurately, we can make safer predictions of future range shifts and their consequences for biodiversity.

Mangroves are a complex of trees, shrubs and ferns adapted to the intertidal zone (Tomlinson 1986). Hence, in comparison with the distribution of terrestrial forest types, mangrove ranges are restricted to narrow strips following coast lines. Mangrove tree species are mainly tropical and occur on either side of the equator (Duke et al. 1998; Ellison 2002; Spalding et al. 2010). With increasing latitude, the richness of mangrove species decreases (Ellison 2002), and tree height is reported to decline (Woodroffe and Grindrod 1991; Spalding et al. 1997; Duke et al. 1998). Therefore, the upper latitudinal limits of mangrove species in the northern and the southern hemisphere correspond to their respective leading edges (i.e. the forward edges of the range of a species during migration).

The distribution of mangrove species is primarily controlled by direct (sensu Austin and Heyligers 1989) climate-related factors and secondly by disturbance-related factors or regulators (sensu Guisan and Thuiller 2005) such as wind, coastal hydrology (wave energy and tidal system) and coastal geomorphology (topography, substrate type and soil conditions including salinity and indirect effects on nutrient levels). Interestingly, mangrove species can cover wide ranges along gradients of disturbance factors. Indeed, these species are well distributed along gradients of salt concentration (from oligohaline to hyperhaline), substrate type (from muddy to sandy sediments) and inundation regime (twice a day to twice a month or even micro-tidal systems). In contrast, the total area covered by mangrove forests is small[1] because the intertidal zone is narrow.

Although the total area of mangrove forests is small, their latitudinal extent is large, ranging from ±32°N to ±38°S. Most resources and conditions that mangroves require do not vary gradually with latitude; however, temperature does (e.g. Barry and Chorley 2004; Rohli and Vega 2007). Therefore, it is expected that the limiting temperature for mangrove species is expressed at their upper latitudinal limits. However, Colwell and Rangel (2009) hypothesized that the realized niche of a species may be smaller than its fundamental niche. This indicates that it is possible that mangroves do not fill their whole potential distribution along the temperature gradient towards higher latitudes. Similar cases of partial range filling have been demonstrated for tree species at high latitude in Europe (see Svenning and Skov 2004; Svenning et al. 2010).

Mangrove dispersal and establishment beyond the current distribution limits is a complex dynamic (Tomlinson 1986) depending on three groups of factors: (1) characteristics of the propagules, (2) characteristics of the vector, i.e. surface water currents, and (3) characteristics of the available coastline. The propagules of each mangrove genus have similar shape and anatomical structure but can be largely different among mangrove genera (e.g. see propagules of *Avicennia* compared to *Rhizophora*). The surface water currents vary in time and space depending on the tidal and coastal currents, the winds, and the ocean currents. Ultimately, settling beyond the current distribution requires available coastline and a suitable environment for mangrove establishment.

Like all trees, mangroves are influenced by air temperature (AT) and soil temperature. Air temperature and its effect on relative humidity determine evapotranspiration and stomatal conductance (Robertson and Alongi 1992) as well as wood formation (Fonti et al. 2007; Gricar et al. 2006). Soil temperature influences the growth of roots and the above ground metabolism (DeLucia 1986; Day et al. 1991; Körner and Paulsen 2004). Among the environmental factors available, sea surface temperature (SST) is the variable that is supposed to correlate the best with soil temperature because of tidal inundations and is also known to have an attenuating effect on the air temperature (e.g. Rohli and Vega 2007).

The most recent and widely cited statement about global mean temperature at latitudinal mangrove limits is that of Duke et al. (1998). These authors declared that mangroves require a mean winter SST of at least 20 °C, with exceptions in Brazil, Australia and New Zealand, where winter SST is lower. In that study and others (Macnae 1963; Chapman 1977; Barth 1982; Woodroffe and Grindrod 1991), the datasets of temperature used were either more than 30 years old or the source was not mentioned. Thus, a more detailed and updated approach is necessary focussing on both the mangrove ecosystem level and mangrove genus level.

Apart from global mean limiting factors, extreme stochastic events can locally affect the latitudinal limits of organisms (Woodroffe and Grindrod 1991). At Cedar Key, Florida, the frost tolerance level of the mangrove tree *Avicennia germinans* (L.) Stearn is between −4 and −6.7 °C (Stevens et al. 2006). Both freezing intensity and the frequency of frost events will influence mangrove survival. The series of winters with frost events between 1977 and 1989 in Florida resulted in catastrophic mangrove destruction, while the freezing events in 1995–1996 killed only 4–12 % of the mangrove trees; the remaining mangroves were flowering again in the spring of 1997 (Stevens et al. 2006). At a global scale, the effect of extreme cold events on mangrove latitudinal limits and the potential interplay of other environmental factors remain unclear.

In this study, our intention was to provide new insights in the drivers of the upper latitudinal limits of the

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[1] Recent inventories reported a current surface ranging from 137,760 km$^2$ (Giri et al. 2011) to 152,000 km$^2$ (according to Spalding et al. 2010). However, the original mangrove surface is estimated to have been more than 200,000 km$^2$ before deforestation by man (Valiela et al. 2001; FAO 2003; Duke et al. 2007); this value is two orders of magnitude less than the surface covered by tropical rainforest (Millennium Ecosystem Assessment 2005).

mangroves with an empirical and correlative approach. We assessed the relationships between two temperature-based factors, namely air temperature and sea surface temperature, with the limits of the mangrove genera *Avicennia* L. and *Rhizophora* L. worldwide. We considered the limits of mangrove genera instead of species because no mangrove species is longitudinally pan-tropical, while mangrove genera are (Spalding et al. 1997, 2010) and to ensure statistical power. Moreover; ecological, physiological and morphological traits (e.g. salinity tolerance, leaf type and aerial root system), and ecosystem functions (e.g. wave energy protection) are very similar for congeneric mangrove species. Hence, range differences and complementarity between congeneric mangrove species are assumed to be due to vicariance and allopatric evolution rather than the selective pressure of ecological conditions (Ellison et al. 1999). Worldwide, the upper latitudinal limits of the mangrove ecosystem coincide well with the upper latitudinal limits of the genus *Avicennia* (Spalding et al. 1997, 2010).

More specifically, our objectives were: (1) to indentify the worldwide latitudinal limits for the genera *Avicennia* and *Rhizophora* and, (2) to characterize the monthly SST and AT at these limits. We tested the following two hypotheses: (i) monthly mean AT or SST is the global limiting factor that determines upper latitudinal range limits of the mangrove genera *Avicennia* and *Rhizophora*. Alternatively, if AT and SST do not explain the current leading edge limits of the two genera worldwide, other factors such as dispersal limitation could explain the partial filling of the potential geographic range. We tested one dispersal limitation, namely whether the limited availability or the absence of coast beyond the latitudinal limit is related to warmer temperature at the latitudinal limit. (ii) *Avicennia* can tolerate colder monthly mean AT and SST than *Rhizophora*, explaining why *Avicennia* has higher latitudinal limits.

## Methods

### Defining upper latitudinal limits of the mangrove genera *Avicennia* and *Rhizophora*

The upper latitudinal limits of the mangrove genera *Avicennia* and *Rhizophora* reported by Woodroffe and Grindrod (1991) were used as initial base data for this study. We updated the information provided by these authors with more recent and detailed information about (i) the identity of the species forming the latitudinal limit of a particular genus and (ii) the exact name and coordinates of the sites where the limits are reached. This information was gathered from the literature, contact persons (in 2009–2010) and by personal observations (Mauritania, January 2009). We focused on natural limits, disregarding planted mangrove forests. We checked the presence of mangroves at every limit by a visual interpretation of the satellite images and/or aerial photographs of Google Earth (earth.google.com) and photographs at Panoramio (http://www.panoramio.com).

We selected the two mangrove genera *Avicennia* and *Rhizophora* that are represented in all tropical biogeographical regions. *Avicennia* has been reported to have the widest observed latitudinal range of all mangrove genera (Spalding et al. 1997, 2010). Both genera fulfil many typical mangrove ecosystem functions as breeding and nursing grounds for marine organisms and shoreline protection against storms and floods (Dahdouh-Guebas et al. 2000, 2005; Moberg and Rönnbäck 2003; Barbier 2007; Duke et al. 2007). According to Polidoro et al. (2010), the upper latitudinal limits of *Avicennia* are set by three species (out of eight): *A. marina* (Forssk.) Vierh*., A. germinans* (L.) Stearn and *A. schaueriana* Stapf & Leechm. ex Moldenke (found at 12, 8 and 1 latitudinal limit(s) of *Avicennia* genus, respectively). The species involved in the *Rhizophora* latitudinal limits are *R. mangle* L., *R. racemosa* G.Mey., *R. mucronata* Lam. and *R. stylosa* Griff. (found at nine, two, four and five latitudinal limits of the *Rhizophora* genus, respectively). Except for *A. schaueriana*, all species define latitudinal limits in both hemispheres.

### Explanatory climatic variables

We first generated a set of climate variables for all the upper latitudinal limits of *Avicennia* and *Rhizophora*: monthly mean sea surface temperature (SST), air temperature (AT) and precipitation (P). To have comparable climate data for the different limits worldwide, we used monthly mean values extracted from global datasets. Air temperature and precipitation were taken from the CRU CL 2.0 database (New et al. 2002; 10 × 10 arcmin spatial resolution; obtained from Climate Research Unit, Norwich, UK, http://www.cru.uea.ac.uk), whereas SST was obtained from the NOAA OI SST V2 database (Reynolds et al. 2005; 1° × 1° spatial resolution, National Oceanographic and Atmospheric Administration, Cooperative Institute for Research in Environmental Sciences (NOAA-CIRES), Climate Diagnostics Center, Boulder, CO, USA). Air temperature and precipitation at the limits in Bermuda were taken from the meteorological station at L.F. Wade International Airport (http://www.weather.bm) because this island was not represented in any of the global CRU geographic datasets. The standard climate period of 1961–1990 was used for AT and P, whereas the period 1971–2000 was used for SST.

**Table 1** Acronyms of the temperature-based variables

|  | Air temperature | Sea surface temperature |
| --- | --- | --- |
| Coldest month | $AT_C$ | $SST_C$ |
| Yearly mean | $AT_A$ | $SST_A$ |
| Warmest month | $AT_W$ | $SST_W$ |

We then derived six temperature-based variables (yearly mean temperature ($T_A$), mean temperature of the coldest month ($T_C$) and mean temperature of the warmest month ($T_W$)) from both monthly values of AT and SST. We subsequently used $AT_A$, $AT_C$, $AT_W$, $SST_A$, $SST_C$, and $SST_W$ as acronyms for yearly mean, coldest month and warmest month of AT and SST, respectively (see Table 1). Next, we calculated the minimum, maximum and average values of the six variables derived from AT and SST across all the upper latitudinal limits of the two mangrove genera. To define the minimum temperature requirements of *Avicennia* and *Rhizophora*, we compared these six temperature-based variables among the latitudinal limits of the genera and calculated the temperature variation at the latitudinal limits per genus. Correlating temperature variables with species distribution or range limits has already been used successfully to characterize temperature at the treeline worldwide (Körner and Paulsen 2004) and for freezing resistance (e.g. Sakai 1970). Next, we compared these six temperature-based variables of the *Avicennia* limits with the *Rhizophora* limits with a Mann–Whitney *U* test. We finally derived the yearly temperature range, $AT_R$ and $SST_R$ from the monthly values of AT and SST, respectively.

Response variables

We generated a set of response variables, related to (i) the geographic positions of the upper latitudinal limit, (ii) the species of the studied mangrove genera and (iii) the aridity at the limits. We first verified whether temperature variation between limits was related to partial range filling of their leading edges. With a Mann–Whitney *U* test we tested whether the six temperature-based variables were different according to the position of the limit, i.e. the hemisphere, the biogeographic region and the availability of coast in the vicinity of the mangrove latitudinal limits. The distribution of mangroves can be separated into two biogeographic regions according to species composition. The Indo-West Pacific region (IWP) is species rich with at least thirty-five true mangrove species whereas the Atlantic East Pacific region (AEP) only has eight species (as explained in e.g. Duke et al. 1998). *Avicennia* and *Rhizophora* are the only mangrove genera that have species in both biogeographic regions.

Partial range filling can be caused by dispersal limitation. Beside efficient dispersal properties intrinsic to the studied genera and appropriate surface water currents as the main dispersal vector, the first requirement for establishment is the availability of coast further poleward. We classified the latitudinal limits into two groups: limits with coastal stretches available for the next 250 km poleward and limits with no or less than 250 km coast poleward. Because the distance of 250 km was chosen arbitrarily—but the value is reasonable as the longevity of *Rhizophora* propagules can be 150 days (Dexler 2001) which means an average velocity of 1.7 km per 24 h to cover a distance of 250 km, we conducted a sensitivity analysis for distances varying from 200 to 300 km with 50 km steps. While this is a very simplistic analysis on available coast, taking realistic dispersal processes and barriers into account was impossible without detailed knowledge of the coastal geomorphology and the surface water currents. Such information was unfortunately not available for the majority of the mangrove limits (but see e.g. De Lange and De Lange 1994 in New Zealand, Soares et al. 2012 in Brazil). Finally, sea surface currents can also have a high seasonal variability which further complicates these analyses.

Additionally, we tested the relationship between tree height at the limits and all the temperature-based variables with a Spearman $\rho$ correlation test. Adult tree height is considered as a proxy of relative suitability of a site for a species. Under optimal growth conditions, tree height is 30–50 m for *Rhizophora* and 25–30 m for *Avicennia* (Duke 2006; Duke and Allen 2006; Giesen et al. 2006; FAO 2007). Tree height is reported to decline with increasing latitude (Woodroffe and Grindrod 1991; Spalding et al. 1997). Quality of data collected about adult tree height was not homogeneous. Therefore, we standardised to the median tree height for each site. When only the tree height range was known, we calculated mean tree height from the minimum and maximum and used this value as the median tree height based on the parsimonious assumption that adult tree height of a species in a mangrove forest is normally distributed.

Next, we assessed the relationship between the species forming the limit of a particular genus and the temperature-based variables to test the assumption that congeneric mangrove species forming the upper latitudinal limits of the considered genus have similar minimum temperature requirements for survival (Mann–Whitney *U* test). Finally, we investigated the possible effect of aridity on the minimum temperature requirements of mangroves at their upper latitudinal limits. We used monthly mean AT and P to classify the limits in 'arid or B-climate type limits' and 'non-arid or A/C-climate type limits' based on the Köppen–Geiger classification (Kottek et al. 2006; Peel et al. 2007). We tested if the temperature-based variables were different in both groups with a Mann–Whitney *U* test.

Almost half of the *Avicennia* limits and two-third of the *Rhizophora* limits have an arid B-climate. The non-arid limits have a temperate C-climate, with the exception of three *Avicennia* limits and one *Rhizophora* limit that have a tropical A-climate, the major climate type in the mangrove distribution.

We used non-parametrical statistics (Mann–Whitney *U* test and Spearman $\rho$ correlation test) as the data did not fulfil the requirements for parametrical statistics. All analyses and figures were produced with the R software package (http://www.R-project.org).

## Results

The six temperature-based variables, namely yearly mean temperature ($T_A$), mean temperature of the coldest month ($T_C$) and mean temperature of the warmest month ($T_W$) from both monthly values of air (AT) and sea surface temperature (SST), differed between latitudinal limits of the mangrove genera *Avicennia* and *Rhizophora* (Fig. 1). These temperature variations were generally large. They were larger for AT than for SST and among *Avicennia* (>10.2 °C) than among *Rhizophora* limits (>7.2 °C) (Table 2). The yearly temperature range ($T_R$) of AT and

SST was also highly variable among the latitudinal limits of the two mangrove genera. $SST_R$ at the limits of *Avicennia* varied between 4.3 °C and 13.8 °C and $AT_R$ between 6.2 °C and 20.6 °C. Similar differences were found among *Rhizophora* limits ($SST_R$: 4.3 °C–13.2 °C and $AT_R$: 3.8 °C–15.8 °C).

Overall, the genus *Rhizophora* had a slightly smaller latitudinal extent than *Avicennia*; the median latitudinal geographic distance between *Avicennia* and *Rhizophora* limits was 1.8° or ca. 200 km (Fig. 2). At the global scale, the temperature difference between *Avicennia* and *Rhizophora* limits was only significant for $SST_C$, which is warmer at *Rhizophora* limits (median, 20.8 °C) than at *Avicennia* limits (median, 18.7 °C) (Mann–Whitney *U* test, $n = 18$, $P = 0.046$). More regionally, coldest month and yearly mean AT and SST at the *Rhizophora* limit were warmer than at the nearby *Avicennia* limit along the same coastline (Fig. 1).

The upper latitudinal limits of the mangrove genera *Avicennia* and *Rhizophora* had significantly warmer $AT_W$ and $SST_W$ in the northern hemisphere than in the southern hemisphere (as shown for $AT_W$ in Fig. 3). At *Avicennia* limits, also $AT_A$ and $SST_A$ were warmer at the limits in the northern hemisphere than in the southern hemisphere (Table 3). We found that the *Avicennia* limits in the IWP
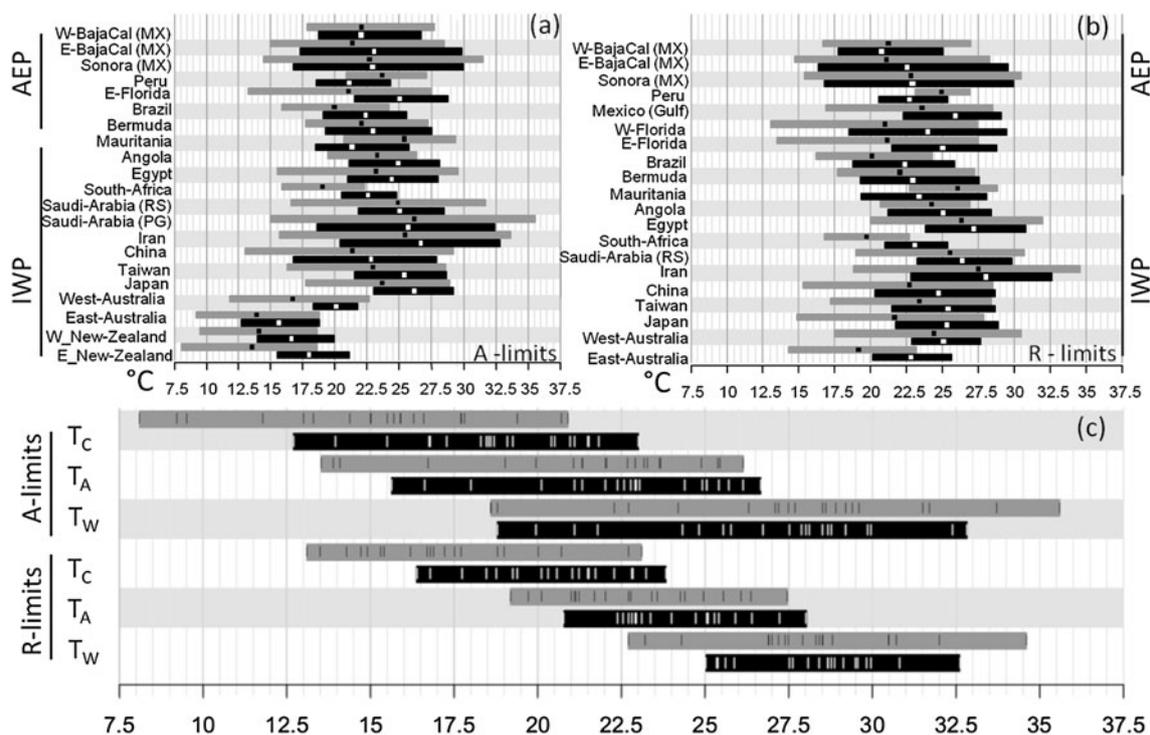


**Fig. 1** **a**, **b** Monthly mean sea surface temperature (SST) (*black box*) and air temperature (AT) (*grey box*) at every *Avicennia* (A) and *Rhizophora* (R) upper latitudinal limit: mean temperature of the coldest month ($T_C$) and warmest month ($T_W$) are the left and right border of the box, respectively, yearly mean temperature ($T_A$) is shown by a white square. **c** $T_C$, $T_A$ and $T_W$ of AT (*grey box*) and SST (*black box*) of all A- respectively R-limits together (*vertical lines*) showing the temperature variation among the mangrove limits. AEP: Atlantic East Pacific Region; IWP: Indo-West Pacific Region

**Table 2** Temperature variation among mangrove limits: minimum (Min., temperature of the coldest limit), mean and maximum (Max., temperature of the warmest limit) temperature of all *Avicennia* and *Rhizophora* latitudinal limits and temperature variation (T Var = Max. − Min.) among the limits

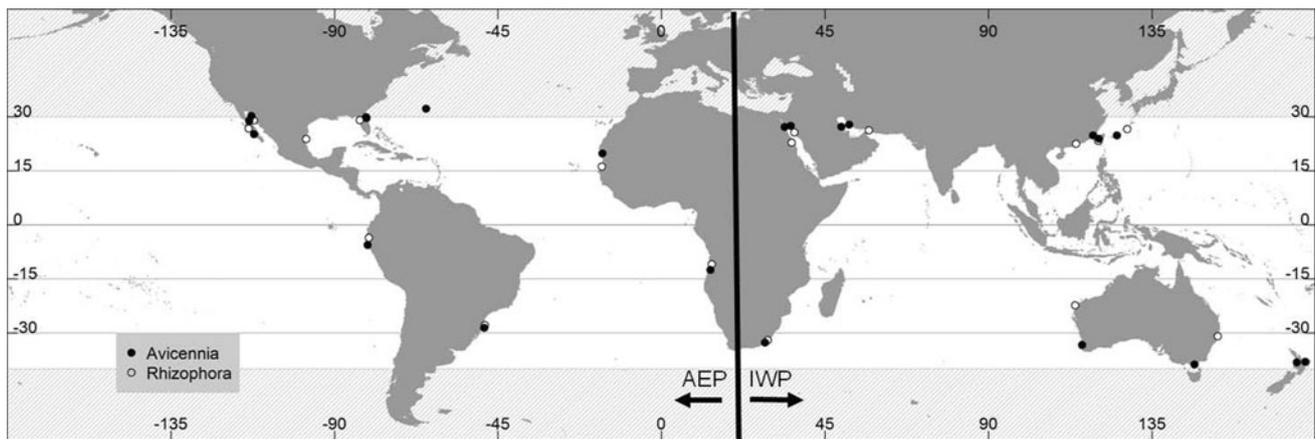| *Avicennia* | $AT_C$ | $SST_C$ | $AT_A$ | $SST_A$ | $AT_W$ | $SST_W$ |
|---|---|---|---|---|---|---|
| Min. (°C) | 8.1 | 12.7 | 13.5 | 15.6 | 18.6 | 18.8 |
| Mean (°C) | 15.2 | 18.8 | 21.2 | 22.6 | 27.0 | 26.7 |
| Max. (°C) | 20.9 | 23.0 | 26.1 | 26.7 | 35.6 | 32.8 |
| T Var (°C) | 12.8 | 10.3 | 12.6 | 11.1 | 17.0 | 14.0 |
| *Rhizophora* | $AT_C$ | $SST_C$ | $AT_A$ | $SST_A$ | $AT_W$ | $SST_W$ |
| Min. (°C) | 13.1 | 16.4 | 19.2 | 20.8 | 22.7 | 25.0 |
| Mean (°C) | 17.2 | 20.5 | 22.9 | 24.3 | 28.1 | 28.3 |
| Max. (°C) | 23.1 | 23.8 | 27.5 | 28.0 | 34.6 | 32.6 |
| T Var (°C) | 10.0 | 7.4 | 8.3 | 7.2 | 11.9 | 7.6 |

Abbreviations follow Table 1



**Fig. 2** World map of the mangrove latitudinal limits for the genera *Avicennia* (*full dots*) and *Rhizophora* (*open dots*), based on Table S1. AEP: Atlantic East Pacific Biogeographic Region; IWP: Indo-West Pacific Biogeographic Region

had colder $AT_C$ than the limits in the AEP and *Rhizophora* limits of the IWP had a significantly warmer coldest month and yearly mean SST than the limits in the AEP (Table 3). At eight out of 21 *Avicennia* limits and four out of 20 *Rhizophora* limits there was less than 250 km coast available beyond the limits poleward (Table S1). However, no significant differences were found for the six temperature-based variables between the *Avicennia* limits with a stretch of 250 km available coast polewards and the other *Avicennia* limits (Table 3; Figure S2). We did not repeat this analysis for *Rhizophora* as the more poleward upper latitudinal limits of *Avicennia* indicate coast with a suitable geomorphology for mangroves beyond the present *Rhizophora* limits. The same analysis for 200 and 300 km stretches did not change the results.

Adult tree height differed between the upper latitudinal limits of the mangrove genera. At their respective limits, *Avicennia* had a lower tree height than *Rhizophora*, with an average difference of 1.2 ± 1.0 m (Table S1). No general correlations were found between tree height and any of the temperature-based parameters derived from AT or SST at the limits. However, at the coldest *Avicennia*, but not *Rhizophora*, limits given by each temperature-based parameter, tree heights were smaller than the median tree height (i.e. less than 2.7 m) (Table S1; Fig. 1).

Species-specific temperature tolerances of the mangrove species that form the upper latitudinal limits of a particular genus cannot explain the large variation of the temperature-based variables among the limits. For the majority of the temperature-based variables, there was no difference between the limits of a particular genus when classified by species. Of all temperature-based variables, only $AT_C$ was colder for the group of *Avicennia* limits formed by the species *A. marina* than by *A. germinans* (Fig. 4a; Table 3). The limit of *A. schaueriana* showed temperatures within the range of temperature variations of the other two *Avicennia* species. The only temperature differences for the *Rhizophora* species limits were a colder coldest month and annual mean SST at the *R. mangle* limits (as shown for $SST_C$ in Fig. 4b; Table 3).

Finally, $AT_A$, $AT_W$ and $SST_W$ were warmer for *Avicennia* limits with an arid climate than for those with a
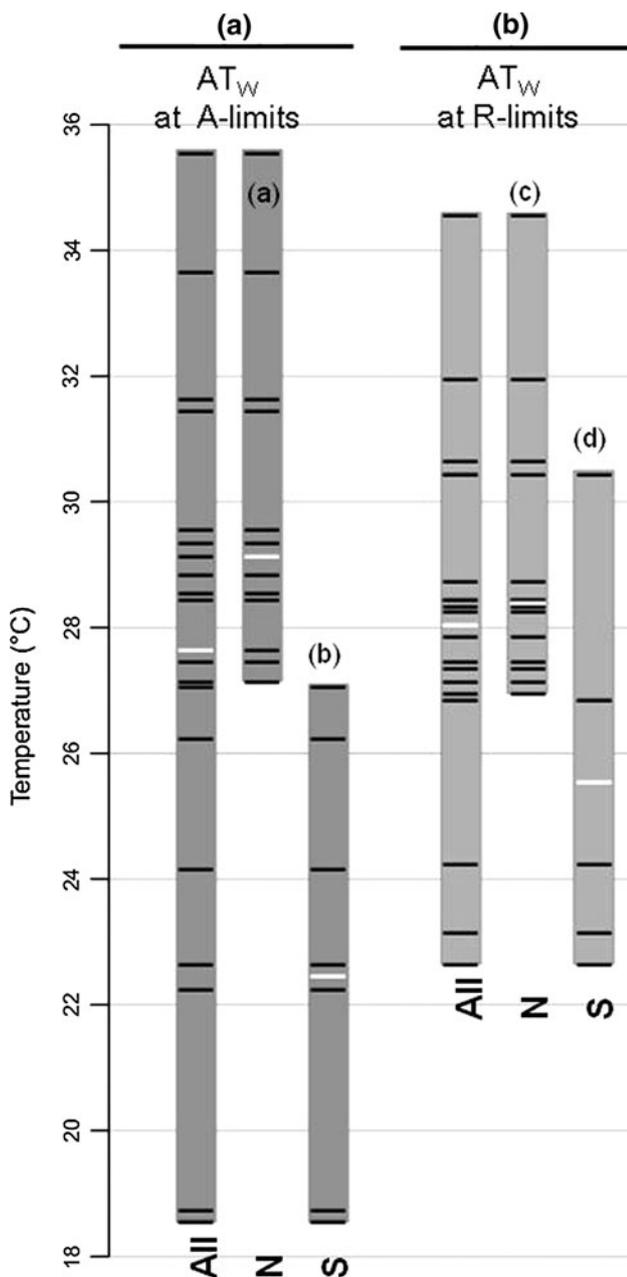
Fig. 3 Temperature at limits grouped by hemisphere. **a**, **b** Mean air temperature of the warmest month ($AT_W$) at upper latitudinal limits of *Avicennia* (A) and *Rhizophora* (R), respectively. N: northern hemisphere, S: southern hemisphere

non-arid climate (Table 3; shown for $AT_A$ in Fig. 5a). Similar compensation of aridity by warmer $AT_A$ at the latitudinal limits was found for *Rhizophora* (Table 3). In addition, $AT_C$ was warmer at *Rhizophora* limits with a desert climate compared to those with a steppe or a non-arid climate type (Fig. 5b).

The latitudinal limits of *Avicennia* and *Rhizophora* which differ from one of the above described findings are summarized and discussed in S3.

## Discussion

### Large temperature variation among latitudinal limits of the mangrove genera *Avicennia* and *Rhizophora*

We found no common isotherms that characterize all upper latitudinal limits for the mangrove genera *Avicennia* and *Rhizophora.* The isotherms were derived from mean air (AT) and sea surface temperatures (SST) of the coldest months ($T_C$), warmest months ($T_W$) and yearly averages ($T_A$). The variation of these six temperature-based variables among latitudinal limits of *Avicennia* and *Rhizophora* was large in comparison with that reported for altitudinal tree limits, despite the greater taxonomic diversity and ecological differences among the species that define the altitudinal limits. Among the 30 altitudinal tree limits distributed worldwide, the variation in mean soil temperature during the growing season is about 4.9 °C (Körner and Paulsen 2004) compared to at least 10.3 °C among *Avicennia* limits and at least 7.2 °C among *Rhizophora* limits for AT and SST derived variables. The range limits of coral reefs also have lower temperature variability than the upper latitudinal limits of the studied mangrove genera, despite their much wider set of structuring species. Worldwide, among the high latitude (>28° latitude) coral reefs, the variability of yearly minimum SST is ±6 °C (Kleypas et al. 1999). Because of the large variation in temperature-based factors observed at the latitudinal limits of *Avicennia* and *Rhizophora*, the temperatures reported in the literature that limit the global mangrove distribution (Table S4) cannot be confirmed. The majority of the *Avicennia* and *Rhizophora* limits are effectively warmer than the temperature values reported in the literature, whereas the limits in Australia and New Zealand are colder. Hence, we can reject our first hypothesis that "monthly mean air temperature or sea surface temperature are the global limiting factors that determine upper latitudinal range limits of the mangrove genera *Avicennia* and *Rhizophora*".

Like the mean temperature at the latitudinal limits of *Avicennia* and *Rhizophora*, the yearly temperature range ($T_R$) at each limit is highly variable. At several limits, the $T_R$ is much higher, up to 20.6 °C, than the maximum $T_R$ of 10 °C for extensive mangrove development proposed by Chapman (1977). Although mangrove forests at their latitudinal limits are mostly not extensive, it is important to note the flexibility of the ecosystem towards a large $T_R$.

One reason that could explain the variation in temperature-based variables among the upper latitudinal limits of *Avicennia* and *Rhizophora* is that mangroves may not occupy all climatically suitable habitats towards higher latitudes (Colwell and Rangel 2009). Therefore, this high temperature variation can be due to partial range filling towards the leading edge limits, which is supported by the

fact that the limits of the two mangrove genera in the northern hemisphere have warmer $AT_W$ and $SST_W$ than in the southern hemisphere. Partial range filling is suggested for *R. stylosa* at its southern latitudinal limit in eastern Australia based on phenologies of leaf gain and leaf loss and the rate of growth assessed by leaf initiation (Wilson and Saintilan 2012). Numerous studies have reported evidence for limited filling of the potential geographic range for many tree species in Europe (e.g. Svenning and Skov 2004; Willner et al. 2009) and elsewhere (Schurr et al. 2007). Disregarding the complex dispersal process itself, we tested whether dispersal limitation by the absence of coast beyond the latitudinal limit is related to warmer temperature at the latitudinal limit. This is not the case: temperature parameters are not warmer at *Avicennia* limits with no or limited (less than 250 km) coast available further polewards than at other limits.

Adult tree height, which has been considered as an indicator of the suitability of growing conditions (Takyu et al. 2005; Lovelock et al. 2006; Naidoo 2006; Hertel and Wesche 2008; Li et al. 2010), is not correlated with the temperature parameters at the limits. However, while tree height within one mangrove forest can be highly variable due to soil conditions (e.g. McKee 1993; Naidoo 2006), the shorter trees at the latitudinal limits (<2.7 m) compared to under optimal growth conditions [i.e. 30–50 m for *Rhizophora* and 25–30 m for *Avicennia* (Duke 2006; Duke and Allen 2006; Giesen et al. 2006; FAO 2007)] suggests that temperature may partly control the latitudinal limits of these genera.

The large temperature variation among the latitudinal limits of both mangrove genera cannot be explained by the fact that these limits are formed by different species per genus. Only *R. mangle* and *A. marina*, contributed to the variation in some of the temperature parameters (Table 3) at the latitudinal limits of the mangrove genera. Temperature differences found between the latitudinal limits of the two biogeographic regions, however can be fully explained by the specific temperature tolerances of *R. mangle* and *A. marina*.

Aridity strengthens the minimum temperature requirements of *Avicennia* and *Rhizophora* at their upper latitudinal range limits. In arid conditions mangroves cannot withstand a low yearly mean air temperature. Only a low sea surface temperature, which is the temperature that is experienced at the roots, and short periods of cold air temperatures can be supported. The level of aridity determines the coldest month air temperatures that *Rhizophora* can tolerate, dividing the *Rhizophora* limits into warm limits with a desert climate and colder limits with a steppe or non-arid climate. Drought stress in the mangrove habitat is always coupled to salinity stress (Medina and Francisco 1997). Rainfall lowers soil water salinity (Robert et al.

2009) and creates a higher relative humidity. Although no studies have been reported to date on the effects of salinity and temperature interactions on mangrove physiology, the negative impact of hypersaline conditions is clear (Ball and Farquhar 1984; Ball 1998; Sobrado 1999; Hao et al. 2009; Feller et al. 2010).

We assume that monthly mean temperatures reflect a biologically relevant magnitude. However, an organism faces and integrates the permanently changing actual temperatures instead of a monthly average. It is well known that thermal extremes are more decisive than means in explaining plant distribution. Extreme cold events such as frost, even for a short duration, also have a direct impact on mangroves, as summarised in Woodroffe and Grindrod (1991) and Krauss et al. (2008) e.g., the forests will experience dieback. Frost events are numerically incorporated in the mean temperature of the coldest month. However, inferring absolute minima from lowest monthly mean temperature is not accurate, because in a coastal setting temperature extremes are strongly defined by the predominant wind direction and local climate conditions. Sea-to-land winds prevent freezing whereas land-to-sea winds increase the likelihood of freezing during cold spells. Unfortunately, information about freezing events are difficult to obtain at the required local level (e.g. exact length and frequency, but see Lugo and Zucca 1977; Sakai and Wardle 1978; Woodroffe and Grindrod 1991; Stevens et al. 2006; Stuart et al. 2007; Krauss et al. 2008). Local climate records are not available for the majority of the latitudinal limits we studied. Therefore, we could not incorporate frost events in our study.

### Colder temperatures at *Avicennia* limits than at *Rhizophora* limits

We found support for our second hypothesis, that *Avicennia* can tolerate colder monthly mean temperatures than *Rhizophora*, explaining *Avicennia*'s larger latitudinal extent. Along the same coastline, coldest month and yearly mean AT and SST at the *Rhizophora* limit are warmer than at the nearby *Avicennia* limit. *Avicennia*'s tolerance for lower temperatures than those tolerated by any other mangrove genus is explained by the less strict environmental requirements of *A. marina* and *A. germinans*. Both species have broad latitudinal and longitudinal ranges, and can cope with a wide range of environmental conditions within one forest, such as wide variations in salinity (Clough 1984; Ball 1988; Dahdouh-Guebas et al. 2004; Ye et al. 2005; Sobrado and Ewe 2006; Robert et al. 2009).

One strategy of *Avicennia* to deal with extreme environmental conditions might be to lower tree height to increase the tree's cost-efficiency (Westoby et al. 2002; Zhang et al. 2009). In general, *Avicennia* was shorter

**Table 3** $P$ values of Mann–Whitney $U$ tests for coldest month ($T_C$), yearly mean ($T_A$) and warmest month ($T_W$) air temperature (AT) and sea surface temperature (SST) at the latitudinal limits of *Avicennia* and *Rhizophora* grouped by hemisphere, biogeographic region, availability of coast for the next 250 km further polewards, species and aridity

| *Avicennia* | N (13)–S (8) | | | AEP (9)–IWP (12) | | | NoCoast (7)–coast (14) | | | A.ger (8)–A.mar (12) | | | Arid (10)–non-arid (11) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Limits | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ |
| AT $P$ | n.s. | <0.001 | <0.01 | <0.05 | n.s. | n.s. | n.s. | <0.01 | <0.01 | <0.05 | n.s. | n.s. | n.s. | <0.01 | <0.01 |
| SST $P$ | n.s. | <0.001 | <0.01 | n.s. | n.s. | n.s. | n.s. | n.s. | 0.01 | n.s. | n.s. | n.s. | n.s. | n.s. | 0.01 |

| *Rhizophora* | N (14)–S (6) | | | AEP (11)–IWP (9) | | | *R. man* (9)–other R-limits (11) | | | Arid (13)–non-arid (7) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Limits | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ | $T_C$ | $T_A$ | $T_W$ |
| AT $P$ | n.s. | n.s. | <0.05 | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | <0.05 | n.s. |
| SST $P$ | n.s. | n.s. | <0.01 | <0.01 | <0.05 | n.s. | <0.01 | <0.05 | n.s. | n.s. | n.s. | n.s. |

The number of limits is indicated between the brackets

*N* northern hemisphere, *S* southern hemisphere, *AEP* Atlantic East Pacific biogeographic region, *IWP* Indo-West Pacific biogeographic region, *NoCoast* No or less than 250 km coastline available further poleward, *Coast* at least 250 km coast available further poleward, *R.man Rhizophora mangle*, *A.ger Avicennia germinans*, *A.mar A. marina*, *n.s.* not significant

compared to *Rhizophora* at their respective limits. Most *Rhizophora* species appear to be unable to form adult trees that are as low and as vigorous as those of *Avicennia* at its latitudinal limits. This finding might be related to *Rhizophora*'s growth form, where prop roots hinder branching shortly above the ground. However, there is one *Rhizophora* species; *R. mangle*, that can form adult trees with tree heights as low as the smallest *Avicennia* trees when resources (e.g. phosphorus) or direct environmental variables (e.g. salinity) are limiting (e.g. Lovelock et al. 2006; Hao et al. 2009; Medina et al. 2010). *R. mangle* has a smaller tree height at the latitudinal limits than the other *Rhizophora* representatives. This can be an advantage for withstanding colder temperatures because temperature differences between the *R. mangle* and *Avicennia* limits (0–2 °C) are smaller than temperature differences between other *Rhizophora* and *Avicennia* limits (0–8 °C).

A second strategy of *Avicennia* is the capacity to sprout after die-back following harsh environmental conditions and even after cutting. This meristematic flexibility can be linked to *Avicennia* having successive cambia leading to a special mechanism for secondary growth while all other mangrove species have regular secondary growth via one vascular cambium (Schmitz et al. 2008; Robert et al. 2011).

### Climate change

Global warming during the 21st century will primarily impact mangrove distribution by sea level rise (Parry et al. 2007; Gilman et al. 2008). However, increasing temperature is also likely to directly affect mangroves at their latitudinal range limits (Gilman et al. 2008). We found no worldwide isotherms for the mangrove latitudinal range limits but a local effect of temperature on the distribution

limits. This is supported by the fact that *Rhizophora* limits are warmer than the nearby *Avicennia* limits, along the same coastline, when all other environmental conditions are similar. Studies on the mangrove latitudinal range borders are thus needed on a local or regional scale to assess potential impacts of global warming. A southwards expansion of the range limits in Brazil is expected by Soares et al. (2012). An increase of AT and SST, a reduction of frost events and a stronger Brazil Current are predicted and sheltered estuarine systems are available along the coast for new mangrove establishment. In South-Africa, Quisthoudt et al. (2012) predicted a southward shift of the latitudinal limits of *A. marina* and *B. gymnorrhiza* (L.) for the end of the 21st century, while the model predicted divergent projections for the latitudinal limit of *R. mucronata.*

### Conclusion

Investigating the environmental factors is a first step towards the full understanding of a species range limits (Gaston 2003). Here, we can conclude that temperature alone, the climate factor that varies the most with latitude, does not define the latitudinal range limits of the mangrove genera *Avicennia* and *Rhizophora*. Both mangrove genera may not have reached their thermal limits towards higher latitudes since mangrove limits have warmer warmest month temperatures in the northern than in the southern hemisphere. This partial range filling is not caused by the absence or limited availability of coast beyond the current limits. Besides, the minimum temperature requirements by *Avicennia* and *Rhizophora* are higher at arid limits than at non-arid limits. Finally, along the same coastline, where all
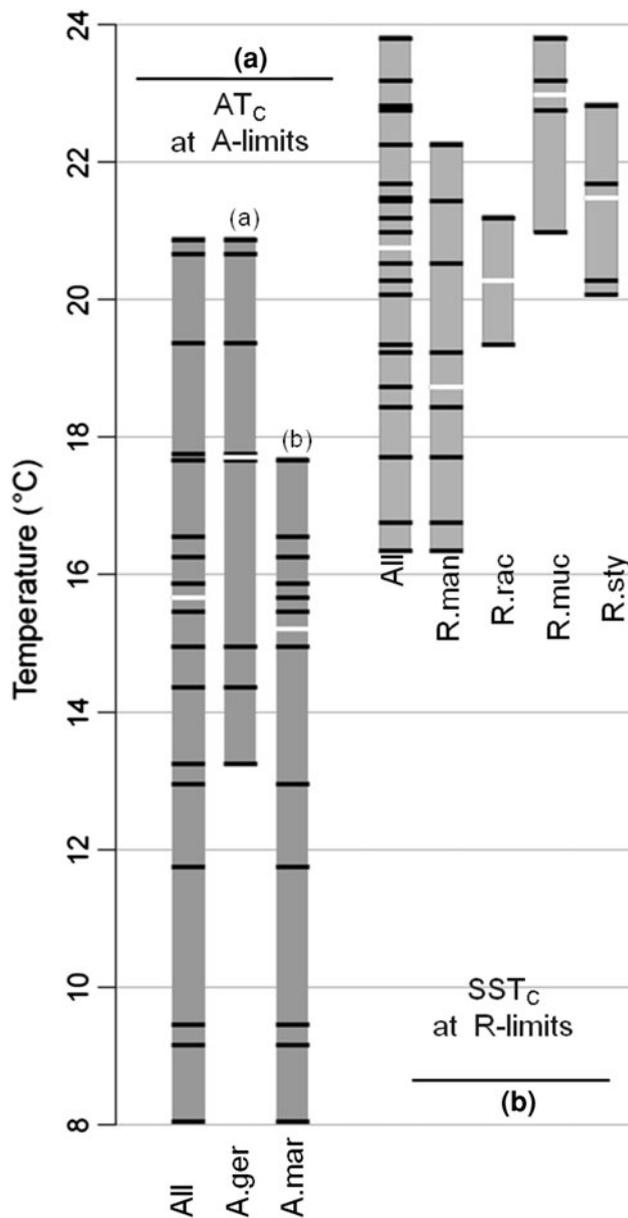
**Fig. 4** Temperature at limits grouped by species. **a** Mean air temperature of the coldest month (AT$_C$) at the *Avicennia* limits per species. **b** Mean sea surface temperature of the coldest month (SST$_C$) at *Rhizophora* limits per species. A.ger: *Avicennia germinans* limits; A.mar: *A. marina* limits; R.man: *R. mangle* limits; R.rac: *R. racemosa* limits; R.muc: *R. mucronata* limits; R.sty: *R. stylosa* limits



**Fig. 5** Temperature at limits with arid versus non-arid climate. **a** Yearly mean air temperature (AT$_A$), **b** yearly mean sea surface temperature (SST$_A$) at *Avicennia* (A) limits, and **c** mean air temperature of the coldest month (AT$_C$) at *Rhizophora* (R) limits. The cold steppe limits are indicated in *lighter grey*

other environmental conditions are similar, temperature does prevent *Rhizophora* from expanding towards the colder *Avicennia* limit. The currently available climate data of the coastal zone, which is on the edge of ocean and land, are derived from limits of either land or ocean climate datasets, where errors are magnified. In addition, mangroves are often found in sheltered bays, where local micro-climates can exist, which are not captured by the spatial resolution of the global datasets. Today,

temperature records collected within the mangrove estuaries do not exist for the majority of the mangrove limits. Specific climate databases for the coastal zones and ultimately even meteorological monitoring in the mangrove forests are therefore welcome to optimize future studies.

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