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## Abstract

Mangrove forests are highly productive tidal saline wetland ecosystems found along sheltered tropical and subtropical coasts. Ecologists have long assumed that climatic drivers (i.e., temperature and rainfall regimes) govern the global distribution, structure, and function of mangrove forests. However, data constraints have hindered the quantification of direct climate-mangrove linkages in many parts of the world. Recently, the quality and availability of global-scale climate and mangrove data have been improving. Here, we used these data to better understand the influence of air temperature and rainfall regimes upon the distribution, abundance, and species richness of mangrove forests. Although our analyses identify global-scale relationships and thresholds, we show that the influence of climatic drivers is best characterized via regional range-limit-specific analyses. We quantified climatic controls across targeted gradients in temperature and/or rainfall within 14 mangrove distributional range limits. Climatic thresholds for mangrove presence, abundance, and species richness differed among the 14 studied range limits. We identified minimum temperature-based thresholds for range limits in eastern North America, eastern Australia, New Zealand, eastern Asia, eastern South America, and southeast Africa. We identified rainfall-based thresholds for range limits in western North America, western Gulf of Mexico, western South America, western Australia, Middle East, northwest Africa, east central Africa, and west-central Africa. Our results show that in certain range limits (e.g., eastern North America, western Gulf of Mexico, eastern Asia), winter air temperature extremes play an especially important role. We conclude that rainfall and temperature regimes are both important in western North America, western Gulf of Mexico, and western Australia. With climate change, alterations in temperature and rainfall regimes will affect the global distribution, abundance, and diversity of mangrove forests. In general, warmer winter temperatures are expected to allow mangroves to expand poleward at the expense of salt marshes. However, dispersal and habitat availability constraints may hinder expansion near certain range limits. Along arid and semiarid coasts, decreases or increases in rainfall are expected to lead to mangrove contraction or expansion, respectively. Collectively, our analyses quantify climate-mangrove linkages and improve our understanding of the expected global- and regional-scale effects of climate change upon mangrove forests.

## Disciplines
Medicine and Health Sciences | Social and Behavioral Sciences

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# Climatic controls on the global distribution, abundance, and species richness of mangrove forests

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*Abstract.* Mangrove forests are highly productive tidal saline wetland ecosystems found along sheltered tropical and subtropical coasts. Ecologists have long assumed that climatic drivers (i.e., temperature and rainfall regimes) govern the global distribution, structure, and function of mangrove forests. However, data constraints have hindered the quantification of direct climate–mangrove linkages in many parts of the world. Recently, the quality and availability of global-scale climate and mangrove data have been improving. Here, we used these data to better understand the influence of air temperature and rainfall regimes upon the distribution, abundance, and species richness of mangrove forests. Although our analyses identify global-scale relationships and thresholds, we show that the influence of climatic drivers is best characterized via regional range-limit-specific analyses. We quantified climatic controls across targeted gradients in temperature and/or rainfall within 14 mangrove distributional range limits. Climatic thresholds for mangrove presence, abundance, and species richness differed among the 14 studied range limits. We identified minimum temperature-based thresholds for range limits in eastern North America, eastern Australia, New Zealand, eastern Asia, eastern South America, and southeast Africa. We identified rainfall-based thresholds for range limits in western North America, western Gulf of Mexico, western South America, western Australia, Middle East, northwest Africa, east central Africa, and west-central Africa. Our results show that in certain range limits (e.g., eastern North America, western Gulf of Mexico, eastern Asia), winter air temperature extremes play an especially important role. We conclude that rainfall and temperature regimes are both important in western North America, western Gulf of Mexico, and western Australia. With climate change, alterations in temperature and rainfall regimes will affect the global distribution, abundance, and diversity of mangrove forests. In general, warmer winter temperatures are expected to allow mangroves to expand poleward at the expense of salt marshes. However, dispersal and habitat availability constraints may hinder expansion near certain range limits. Along arid and semiarid coasts, decreases or increases in rainfall are expected to lead to mangrove contraction or expansion, respectively. Collectively, our analyses quantify climate–mangrove linkages and improve our understanding of the expected global- and regional-scale effects of climate change upon mangrove forests.

*Key words: abundance; climate change; climate gradients; climatic drivers; climatic thresholds; distribution; ecological thresholds; mangrove forests; rainfall; range limit; species richness; temperature.*

## Introduction

Ecologists have long been interested in the influence of climatic drivers (e.g., temperature and precipitation regimes) upon the global distribution, abundance, and diversity of ecosystems (Holdridge 1967, Whittaker 1970, Woodward 1987). Climate-focused ecological research and distribution modeling have been particularly useful for elucidating climatic controls on ecosystem structure and function (Whittaker 1960, Churkina and Running 1998, Jobbágy and Jackson 2000, Dunne et al. 2004,

Guisan and Thuiller 2005, Elith and Leathwick 2009). Within the context of climate change, studies of the ecological effects of climatic drivers are especially important because they can help scientists and environmental managers better anticipate and prepare for the ecological consequences of changing climatic conditions (Glick et al. 2011, Stein et al. 2014). In addition to improved understanding of the influence of changing mean climatic conditions, there is a pressing need to advance understanding of the ecological implications of changes in the frequency and intensity of climatic extremes (e.g., freezing, drought, flooding; Jentsch et al. 2007, Smith 2011, IPCC 2013, Hoover et al. 2014).

In this study, we examined the influence of climatic drivers upon the distribution, abundance, and species

richness of mangrove forests. Mangrove forests are freeze-sensitive tidal saline wetland ecosystems located along sheltered tropical and subtropical coasts across the world (Tomlinson 1986, Woodroffe and Grindrod 1991, Saenger 2002, Alongi 2009, Spalding et al. 2010, Twilley and Day 2012). Mangrove forests support ecosystem goods and services that have been valued at up to US$194000·ha$^{-1}$·yr$^{-1}$ (Costanza et al. 2014). In addition to providing fish and wildlife habitat, mangrove forests protect coastlines, support coastal fisheries, store carbon, provide timber, improve water quality, and provide recreational opportunities (Ewel et al. 1998, Barbier et al. 2011, Lee et al. 2014).

Despite the tremendous ecological and societal value of mangrove forests, the influence of climatic drivers on mangrove forest distribution, structure, and function has not been well quantified in many parts of the world. The mangrove literature contains many valuable observations and well-articulated hypotheses regarding the influence of temperature and rainfall regimes on the distribution, abundance, and diversity of mangrove forests (e.g., Davis 1940, Lugo and Patterson-Zucca 1977, West 1977, Woodroffe and Grindrod 1991, Duke et al. 1998, Saenger 2002, Ross et al. 2009, Saintilan et al. 2009, 2014, Asbridge et al. 2015). Unfortunately, a lack of relevant and easily accessible climate and/or ecological data has meant that many of these relationships have not been fully tested or quantified. Data constraints have sometimes resulted in the use of the best-available surrogate variables. For example, latitude and sea surface temperatures have often been used as proxies for winter air temperature extremes (e.g., Woodroffe and Grindrod 1991, Duke 1992, Twilley et al. 1992, Saenger and Snedaker 1993, Ellison 2002, Alongi 2009, Twilley and Day 2012), sea surface temperatures have been used instead of rainfall (e.g., Duke 1992, Duke et al. 1998), and mean monthly air temperatures have been used as proxies for extreme minimum daily air temperatures (e.g., Quisthoudt et al. 2012, Record et al. 2013, Hutchison et al. 2014, Jardine and Siikamäki 2014, Rovai et al. 2016, Ximenes et al. 2016). Although these surrogate variables are helpful for showing that general relationships are present, the use of proxies can potentially be misleading without adequate discussion and characterization of the relevant physiological mechanisms responsible. Using proxies also makes it difficult to identify ecologically relevant climatic thresholds, which are needed to anticipate and prepare for future change.

In recent years, the quality and availability of global-scale climate and mangrove distribution data have been improving (Polidoro et al. 2010, Spalding et al. 2010, Giri et al. 2011, Osland et al. 2013, Cavanaugh et al. 2014, Armitage et al. 2015). As a result, there is potential to more directly quantify the influence of climatic controls upon mangrove forests. In this study, we used recent climate and mangrove ecological data to investigate the following questions: (1) at the global and regional range limit scale, how do air temperature and rainfall regimes influence the distribution, abundance, and species richness of mangrove forests; (2) given the historic emphasis on sea surface temperatures in portions of the mangrove ecological literature, what are the linkages between sea surface temperatures, air temperatures, and rainfall regimes; and (3) how and where is climate change, in the form of warmer air temperatures and altered rainfall regimes, expected to affect the distribution, abundance, and diversity of mangrove forests?

Although sea surface temperatures are often used to describe the global distribution of mangroves, we postulated that minimum air temperature and mean annual precipitation regimes are more directly relevant variables, and that these two climatic variables would be tightly correlated to sea surface temperatures. These hypotheses stem from a literature review of mangrove range limits across the world (Table 1). Mangrove forests are highly sensitive to freezing and chilling temperatures, which can lead to mortality and/or damage (Lugo and Patterson-Zucca 1977, Woodroffe and Grindrod 1991, Stuart et al. 2007, Lovelock et al. 2016). Our literature review identifies range limits near transitions zones between tropical and temperate climates where mangrove ecologists have noted that winter air temperatures play an important ecological role (in Table 1, see range limits with temperature minima included as a driver). In addition to air temperature extremes (i.e., freeze events), mangrove mortality and/or damage can also be induced by hypersaline conditions, which are most common and intense along arid and semiarid coasts (Saenger 2002, Saintilan et al. 2009, Semeniuk 2013, Asbridge et al. 2015, Lovelock et al. 2016). Our review identifies range limits near transition zones between arid and humid climatic zones where ecologists have noted that precipitation regimes and hypersaline conditions play an important ecological role (in Table 1, see range limits with rainfall included as a driver). Throughout the manuscript, we use the terms rainfall and precipitation interchangeably, as mangroves are not present in regions with large amounts of colder forms of precipitation (e.g., snow or sleet).

We hypothesized that climatic thresholds associated with temperature and rainfall would be lower for mangrove presence than for abundance and/or species richness because mangrove individuals can be present in physically stressful regions (i.e., colder and/or more arid regions) without being abundant or species rich (Fig. 1). For example, along the northern Gulf of Mexico coast, there are three common mangrove species. Within the coldest coastal reaches that contain mangroves, only isolated individuals of the most freeze-tolerant species (*Avicennia germinans*) are present (in these areas, mangroves are present but not abundant or species rich). In contrast, where the frequency and intensity of temperature extremes decreases, all three species (*A. germinans*, *Rhizophora mangle*, and *Laguncularia racemosa*) can be present (in these areas, mangrove forests are present, abundant, and species rich). We expected similar patterns in presence, abundance, and richness to occur at all range limits.

TABLE 1.    The 14 mangrove distributional range limits evaluated in this study.

| Range limit name | Hypothesized climatic driver | Literature sources for hypothesized climatic driver |
|---|---|---|
| Eastern North America (1) | temperature minima | West (1977), Osland et al. (2013), Cavanaugh et al. (2014) |
| Western Gulf of Mexico (2) | rainfall and temperature minima | Lot-Helgueras et al. (1975), Montagna et al. (2011), Osland et al. (2016) |
| Western North America (3) | rainfall and temperature minima | Felger et al. (2001), Turner et al. (2005) |
| Western South America (4) | rainfall (D&H) | West (1977), Woodroffe and Grindrod (1991), Saintilan et al. (2014) |
| Eastern South America (5) | temperature minima (D&H) | Schaeffer-Novelli et al. (1990), Soares et al. (2012), Ximenes et al. (2016) |
| Northwest Africa (6) | rainfall | Woodroffe and Grindrod (1991), Saenger (2002), Spalding et al. (2010) |
| West central Africa (7) | rainfall | Woodroffe and Grindrod (1991), Saenger (2002), Spalding et al. (2010) |
| Southeast Africa (8) | temperature minima (D&H) | Macnae (1963), Saenger (2002), Quisthoudt et al. (2012) |
| East central Africa (9) | rainfall | Saenger (2002), Spalding et al. (2010) |
| Middle East (10) | rainfall and temperature minima | Saenger (2002), Spalding et al. (2010) |
| Eastern Asia (11) | temperature minima | Chen et al. (2010), Wang et al. (2011) |
| New Zealand (12) | temperature minima | Woodroffe and Grindrod (1991), Morrisey et al. (2010) |
| Eastern Australia (13) | temperature minima (D&H) | Saenger (2002), Duke (2006), Stuart et al. (2007), Saintilan et al. (2014), |
| Western Australia (14) | rainfall and temperature minima (D&H) | Saenger (2002), Duke (2006), Semeniuk (2013) |

*Notes:* These range limits are illustrated in Fig. 2, and the numbers in parentheses correspond to the numbers in that figure. In the climatic driver column, (D&H) indicates that dispersal constraints and/or lack of potential habitat are also expected to influence mangrove distributions near that range limit.
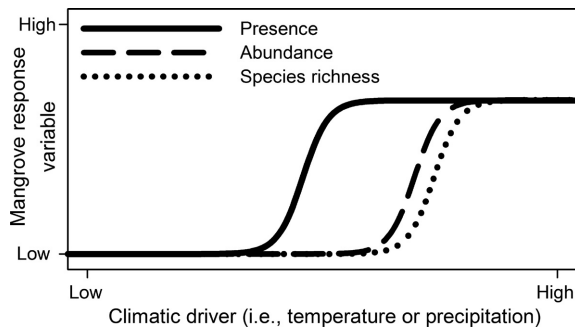


FIG. 1. A generalized illustration of the hypothesized relationships between climatic drivers and mangrove forest presence, abundance, and species richness. The climatic drivers examined in this study include minimum air temperature and mean annual precipitation.

We also expected that global- and regional-scale linkages between climatic conditions and mangroves would be well characterized by nonlinear sigmoidal equations with abrupt ecological thresholds across climatic gradients (Osland et al. 2016). We anticipated that different regional range limits would have different climatic regimes, and that the role of extreme events (e.g., freeze events) would be particularly important in certain regional range limits. For example, mangrove range limits in eastern North America and eastern Australia have different winter air temperature regimes. In eastern North America, winter air temperature extremes are approximately 12°C colder than in eastern Australia; however, annual mean winter air temperatures in eastern North America are occasionally warmer than in eastern Australia. Stuart et al. (2007) noted that, due to these different temperature regimes, mangroves in eastern North America have different growth rates, xylem vessel

diameters, and temperature sensitivities compared to their counterparts in eastern Australian. Winter air temperature and precipitation regimes greatly influence mangrove physiology (Clough 1992, Lovelock et al. 2016), and observations in the literature indicate that freeze and drought sensitivity are range limit dependent (Table 1). Hence, we expected that climatic thresholds for mangrove presence, abundance, and species richness would be range limit specific (i.e., lower in some range limits and higher in others).

## METHODS

### Study area

We first created a seamless global grid of cells with a resolution of 0.5° (i.e., ~50 km at the equator). Next, we created polylines representing coastlines using the perimeter of the Shuttle Radar Topographic Mission (SRTM) v4.1 global digital elevation model data at a resolution of 250 m (Reuter et al. 2007). We used these coastline polylines to identify and retain cells that intersected the coast. We excluded 192227 cells that did not intersect the coast. To avoid cells with minimal potential coastal wetland habitat, we used the SRTM raster data to remove an additional 1056 coastal cells that contained less than or equal to 5% coverage of land. We also removed 176 cells that did not have suitable climate data; most of these cells were removed because they either did not have minimum air temperature data (i.e., no values at all) or they had unrealistic low or high minimum air temperature data relative to their neighboring cells. Collectively, these steps produced a grid (hereafter, study grid) that contained a total of 4908 cells at a resolution of 0.5°.

*Biogeographic zone and range limit assignments*

For biogeographic zone and range-limit-scale analyses, we assigned various identification codes to each study grid cell. Biogeographic zone assignments included either Atlantic East Pacific (AEP) or Indo West Pacific (IWP). These biogeographic zones are described in Duke (1992), Ricklefs and Latham (1993), and Duke et al. (1998), and are included in our analyses because, as for many tropical intertidal and subtidal organisms (e.g., seagrasses, corals), mangrove species richness is much higher in the IWP than the AEP (see also McCoy and Heck 1976, Tomlinson 1986, Woodroffe and Grindrod 1991, Ellison et al. 1999, Ricklefs et al. 2006). In Duke (1992) and Duke et al. (1998), the AEP and IWP are referred to as global hemispheres; however, we have chosen to refer to them as biogeographic zones here. Range limits, defined as areas where mangroves abruptly become absent from coastlines (sensu Gaston 2009, Sexton et al. 2009), were assigned individually using a combination of climate data, mangrove presence data, and descriptions in the literature. We created polygons for 14 focal range limits (Fig. 2), and used these polygons to assign study grid cells to a particular range limit. All range limits spanned a mangrove presence–absence transition. We conducted a literature review to develop hypotheses regarding the climatic and non-climatic factors that control each range limit (Table 1). For range limits that were expected to be controlled, at least in part, by winter temperatures, we created polygons that spanned a temperature transition zone. Where possible, this zone extended from a minimum temperature of −20°C to a maximum minimum temperature of 20°C. However, due to various constraints, most of these transitions covered smaller temperature gradients. For range limits that were expected to be controlled, at least in part, by rainfall, we created polygons that spanned a precipitation transition zone. Where possible, this zone extended from a minimum mean annual precipitation of less than 250 mm up to a maximum mean annual precipitation of greater than 2000 mm. However, due to various constraints, some of these transitions covered smaller precipitation gradients.

*Climate data*

Prior studies in North America have identified the importance of using air temperature extremes in mangrove distribution and abundance models (Osland et al. 2013, Cavanaugh et al. 2014). For all cells within the study grid, we sought to identify the absolute coldest daily air temperature that occurred across a recent multi-decadal period. Although monthly based mean minimum air temperature data are readily available, daily minimum air temperature data have historically been more difficult to obtain at the global scale (Donat et al. 2013). Due to the absence of a consistent and seamless global data set of daily air temperature minima, we used a combination of three different gridded daily minimum air temperature data sources. For

cells in the United States, we used 2.5-arcminute resolution data created by the PRISM Climate Group (Oregon State University; Daly et al. 2008), for the period extending from 1981 to 2010 (data *available online*).[6] For all continental cells outside of the United States (i.e., coastal cells connected to large bodies of land on all continents, but not cells in the United States), we used 1-degree resolution data created by Sheffield et al. (2006), for the same time period. For most islands, we used 0.5-degree resolution data created by Maurer et al. (2009), for the period extending from 1971 to 2000. From these three data sources, we created a minimum temperature (MINT) data set for the study grid cells to represent the absolute coldest air temperature that occurred across a recent three to four decade period, depending upon the source. For each study grid cell, we also obtained 30-s resolution mean annual precipitation (MAP) data from the WorldClim Global Climate Data (Hijmans et al. 2005), for the period extending from 1950 to 2000. In addition to the air temperature and precipitation data, we also obtained sea surface temperature data. Because sea surface temperatures are often used to describe the global distribution of mangrove forests, we wanted to elucidate the relationships between sea surface temperatures, air temperatures, and precipitation. We obtained 5-arcminute resolution global gridded mean annual sea surface temperature data from a data set produced by UNEP-WCMC (2015), for the period extending from 2009 to 2013.

In addition to the gridded climate data, we obtained station-based air temperature data to better characterize winter air temperature regimes within each range limit. We used these data to quantify range-limit-specific differences in the importance of extreme events (e.g., freeze events) relative to typical winter air temperatures. For 13 of the 14 focal range limits, we identified a station with a long-term record of daily air temperatures that was proximate to the mangrove range limit (Appendix S1). For each of these stations, we obtained daily minimum air temperature data for the 30-year period extending from 1981 to 2010. From these data, we calculated (1) the absolute coldest temperature during the 30-yr record (MINT); (2) the annual minimum temperature (i.e., the coldest temperature of each year); and (3) the annual mean winter minimum temperature (i.e., the mean of the daily minima for the coldest quarter of each year). For range limits in the northern hemisphere, the coldest quarter included the months of December, January, and February. For all but one range limit in the southern hemisphere, the coldest quarter included the months of June, July, and August. For the western South America range limit, the coldest quarter included the months of July, August, and September.

*Mangrove data*

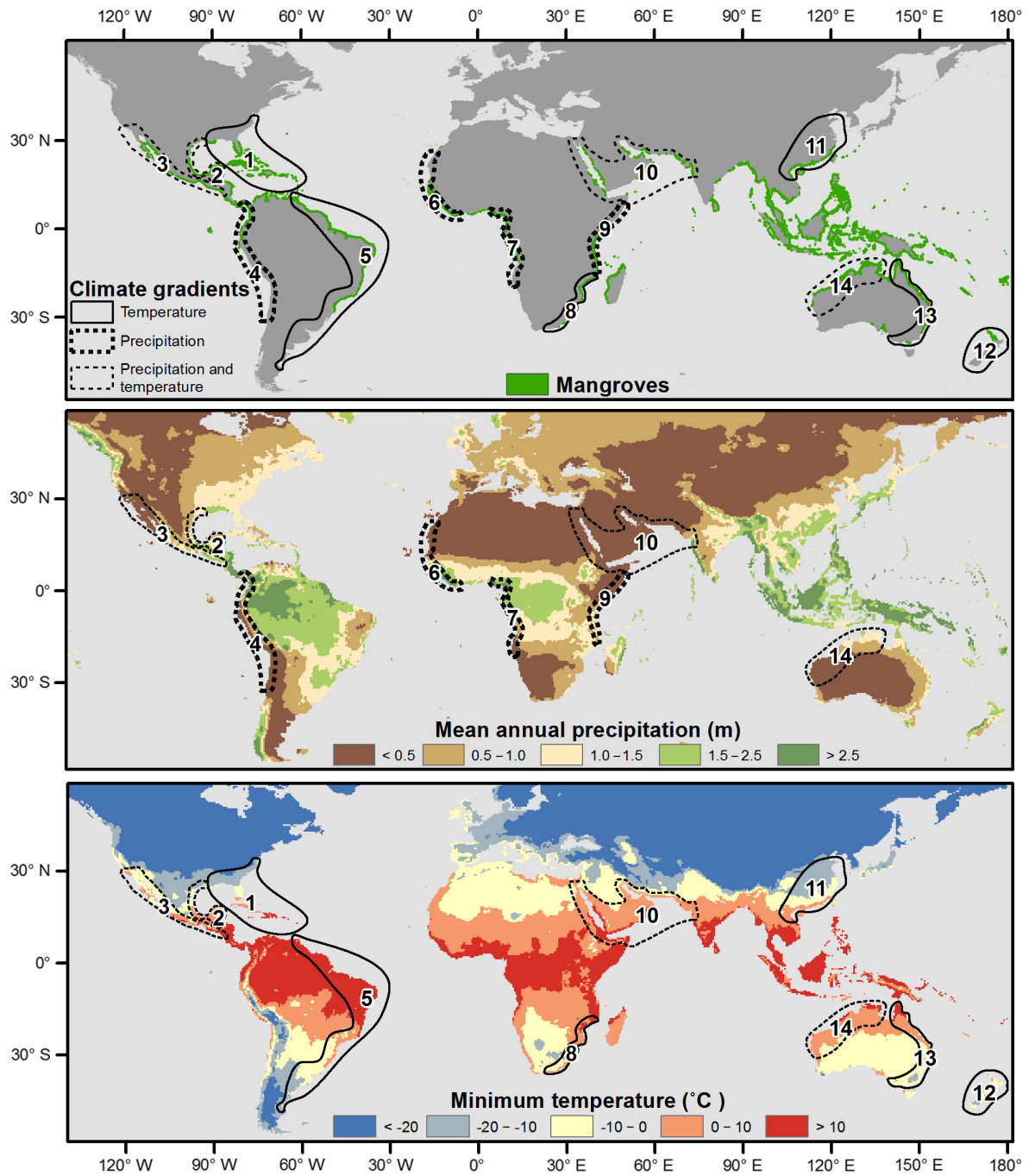To determine mangrove presence, we used two global mangrove distribution data sources (Spalding et al. 2010,

Fig. 2. Maps of (a) the global mangrove distribution and the 14 range limit regions identified in our study (range limits denoted by numbered polygons); (b) mean annual precipitation and the range limit regions containing precipitation gradients; and (c) minimum air temperature and the range limit regions containing temperature gradients. Polygon line styles denote the climatic driver(s) hypothesized to be controlling each range limit, and numbers refer to the range limit names provided in Table 1.

Giri et al. 2011), and assigned a binary code to each study grid cell denoting presence or absence. For most of the world, mangrove presence was assigned to a cell only when both of these sources deemed that mangroves were present (i.e., data conflation; Villarreal et al. 2014). For Myanmar, however, the two mangrove distribution sources were not in agreement (i.e., data were absent from one data set), and the Giri et al. (2011) data were used to assign mangrove presence for those cells. The two sources were also not in agreement for the coasts of Gabon, Congo, and the Cabinda Province of Angola, and the Spalding et al. (2010) data were used to assign mangrove presence for those cells.

For each cell where mangroves were deemed to be present, we used the sum of the species-specific mangrove distributional range data from Polidoro et al. (2010) to determine the total number of mangrove species potentially present within a cell (i.e., mangrove species richness). The Polidoro et al. (2010) data include individual native range distribution polygons for all mangrove species. To determine mangrove abundance (i.e., coverage or area) within each cell, we used the 30-m resolution global mangrove distribution data produced by Giri et al. (2011).

### Data analyses

Data analyses were conducted at the global scale, the biogeographic zone scale, and the range limit scale (see Appendix S2 for a summary of the range-limit-specific analyses that were conducted, Appendix S3 for a discussion of those range-limit-specific analyses, and Appendix S4 for range-limit-specific temperature-precipitation correlations). At the global and range limit scales, we conducted logistic regression analyses using mangrove presence as the dependent variable and MINT or MAP as the independent variable. The inflection point of the logistic equation represents the point of maximum rate of change (i.e., the peak of the first derivative of the equation), and was used to identify climate-based thresholds for mangrove presence. From an ecological perspective, this threshold represents the climatic position with the highest rate of ecological change from one state (e.g., mangrove) to another state (e.g., non-mangrove; salt marsh or salt flat). Near this threshold, small changes in climatic conditions can result in comparatively large ecological change.

We used the cell-based mangrove abundance data to calculate abundance metrics within temperature and precipitation bins (i.e., from the original cells, we calculated abundance values to represent 1°C and 0.1-m intervals for temperature and precipitation, respectively). We used the mangrove area data to calculate mangrove relative abundance for each bin as a percentage (i.e., the percentage of mangrove area present within a bin relative to the total mangrove area present within all bins at the scale of interest). Relative abundance was calculated at global and range limit scales. At the global scale, we conducted sigmoidal regression analyses (Osland et al. 2013, 2014) that included mangrove abundance as the dependent variable and either MINT or MAP as the independent variables. At the range-limit scale, we conducted sigmoidal regression analyses using mangrove abundance as the dependent variable and MINT as the independent variable. For the sigmoidal analyses, we used the inflection points of the sigmoidal equations to identify climate-based thresholds for mangrove abundance. Insufficient data precluded analyses of range-limit-specific relationships between MAP and abundance. Some of the MAP gradients are comparatively abrupt (i.e., they occur over a small area), and we suspect that additional data (e.g., potential habitat data) and/or additional data processing steps (e.g., area-weighted analyses) would be needed to adequately characterize

range-limit-specific MAP-abundance linkages. The abundance analyses would be greatly improved by the incorporation of a mangrove abundance metric that quantified the amount of mangrove area relative to the total tidal saline wetland coverage in a cell (sensu Osland et al. 2013, 2014). Such a metric would better account for additional factors that govern mangrove abundance (e.g., coastal geomorphology, topography, land use change). Unfortunately, a global tidal saline wetland habitat distribution data set has not yet been produced.

Since mangrove species richness is much higher in the IWP biogeographic zone than the AEP zone (Tomlinson 1986, Duke 1992, Ricklefs and Latham 1993, Ellison et al. 1999), our initial species richness analyses were conducted at the biogeographic-zone scale rather than the global scale. For each of the two biogeographic zones, we conducted sigmoidal regression analyses using mangrove species richness as the dependent variable and either MINT or MAP as the independent variables. We also conducted range-limit-specific sigmoidal regression analyses. For the sigmoidal analyses, we used the inflection points of the sigmoidal equations to identify climate-based thresholds for mangrove species richness.

For all 14 range limits, Spearman rank correlations were used to quantify the range-limit-specific linkages between sea surface temperatures and either MINT or MAP. Within eight example range limits, we used bivariate regression analyses, with exponential limited growth functions, to better characterize the relationships between sea surface temperatures and either MINT or MAP. For each of the 14 range limits, linear regression was used to quantify the range-limit-specific correlation between MINT and MAP (Appendix S4). For all analyses, statistically significant relationships were defined as those with a $P$ value less than 0.05. Logistic regression analyses were conducted in R (R Code Team 2016). Sigmoidal regression, exponential limited growth regression, and Spearman rank correlation analyses were conducted in Sigma Plot Version 12.0 (Systat Software, San Jose, California, USA). Maps and geospatial products were created using Esri ArcGIS 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA).

## RESULTS

### Global-scale relationships between climatic drivers and mangroves

At the global scale, there was a significant relationship between mangrove presence and both MINT and MAP (Appendix S5). Mangrove abundance at the global scale was also significantly related to MINT (Fig. 3, upper panel) and MAP (Fig. 3, lower panel). The global-scale thresholds for mangrove abundance were identified to be 7.3°C and 0.78 m for MINT and MAP, respectively. In both the IWP and AEP biogeographic zones, mangrove plant species richness was significantly related to MINT (Fig. 4, upper panels) and MAP (Fig. 4, lower panels).
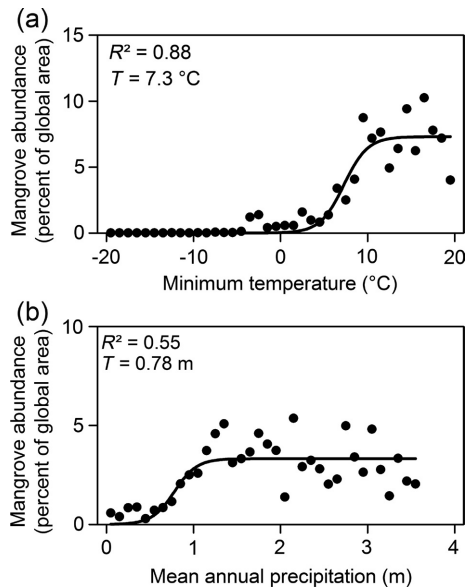
FIG. 3. The global-scale relationships between (a) mangrove abundance and minimum air temperatures and (b) mangrove abundance and mean annual precipitation. Mangrove abundance represents the percentage of the global mangrove area present within a particular temperature or precipitation bin (1°C and 0.1 m bins, respectively). $T$ represents the inflection point or threshold.

Species richness was higher in the IWP than the AEP (Fig. 4). In the IWP, the thresholds for species richness were 8.0°C and 1.48 m for MINT and MAP, respectively (Fig. 4, left panels). In the AEP, the thresholds for species richness were 8.9°C and 1.36 m for MINT and MAP, respectively (Fig. 4, right panels).

### Correlations between sea surface temperatures and climatic drivers

At the range limit scale, there were significant positive relationships between (1) mean annual sea surface temperatures and MINT and (2) mean annual sea surface temperatures and MAP (Fig. 5; Appendix S6). To illustrate these relationships, we present four example range limits for each climatic variable. For eastern North America, eastern Australia, eastern Asia, and eastern South America, we present significant relationships between mean annual sea surface temperatures and MINT (Fig. 5a). For northwest Africa, western North America, western South America, and west-central Africa, we present significant relationships between mean annual sea surface temperatures and MAP (Fig. 5b). Note that many of these relationships have a sea surface temperature asymptote near 20°C (Fig. 5).

### Range-limit-specific differences in winter air temperature regimes

Analyses of the station-based air temperature data illustrate differences between typical and extreme winter air temperatures across range limits (Fig. 6). Eastern North America, western Gulf of Mexico, western North America, and eastern Asia had the lowest absolute temperatures (minimum [Min]: −12.2°, −11.1°, −5.0°, and −3.9°C, respectively) as well as large differences between extreme annual events and typical winter daily minima (difference [Dif]: 12.7°, 12.1°, 8.2°, and 7.7°C, respectively; Fig. 6a–c, k). In New Zealand, southeast Africa, eastern Australia, and the Middle East, the lowest absolute temperatures were −0.7°, −0.5°, 0.1°, and 1.0°C, respectively, and the differences between extreme annual events and a typical winter daily minima were 6.8°, 6.2°, 4.5°, and 7.6°, respectively (Fig. 6l, h, m, j). In eastern South America, the lowest absolute temperature was 0.0°C, and the difference between extreme annual events and typical winter daily minima was relatively large (Dif: 9.3°C; Fig. 6e). In western Australia, the Min and Dif were 2.9° and 6.3°C, respectively (Fig. 6n).

### Range-limit-specific relationships between climatic drivers and mangroves

Climatic thresholds were range limit specific, and within range limits, there were tight linkages between MINT or MAP and the mangrove response variables. There were significant relationships between mangrove presence and MINT in eastern North America, eastern Australia, New Zealand, eastern Asia, eastern South America, and southeast Africa (Fig. 7; MINT-based thresholds for mangrove presence: −7.1°, −2.6°, −2.0°, −0.2°, 5.2°, and 6.9°C, respectively; Appendix S4). There were significant relationships between mangrove presence and MAP in northwest Africa, Middle East, western North America, western Australia, east-central Africa, west central Africa, western Gulf of Mexico, and western South America (Fig. 8; MAP-based thresholds for mangrove presence: 0.32, 0.42, 0.51, 0.54, 0.54, 0.73, 1.05, and 1.28 m, respectively; Appendix S4). There were significant relationships between mangrove abundance and MINT in eastern North America, eastern Australia, New Zealand, eastern Asia, eastern South America, and southeast Africa (Fig. 9; MINT-based thresholds for mangrove abundance: −4.5°, 1.6°, −1.5°, −1.7°, −0.5°, and 9.5°C, respectively). Insufficient data precluded analyses of range-limit-specific relationships between MAP and abundance. There were significant relationships between mangrove species richness and MINT in eastern North America, eastern Australia, New Zealand, eastern Asia, eastern South America, and southeast Africa (Fig. 10; MINT-based thresholds for mangrove species richness: −7.8°, 3.0°, −2.1°, −0.3°, 9.7°, and 8.5°C, respectively). There were significant relationships between mangrove species richness and MAP in northwest Africa, Middle East, western North America, western Australia, east central Africa, west-central Africa, western Gulf of Mexico, and western South America (Fig. 11; MAP-based thresholds for mangrove presence: 0.61, 1.09, 1.00, 0.61, 0.57, 0.49, 1.34, and 0.71 m,
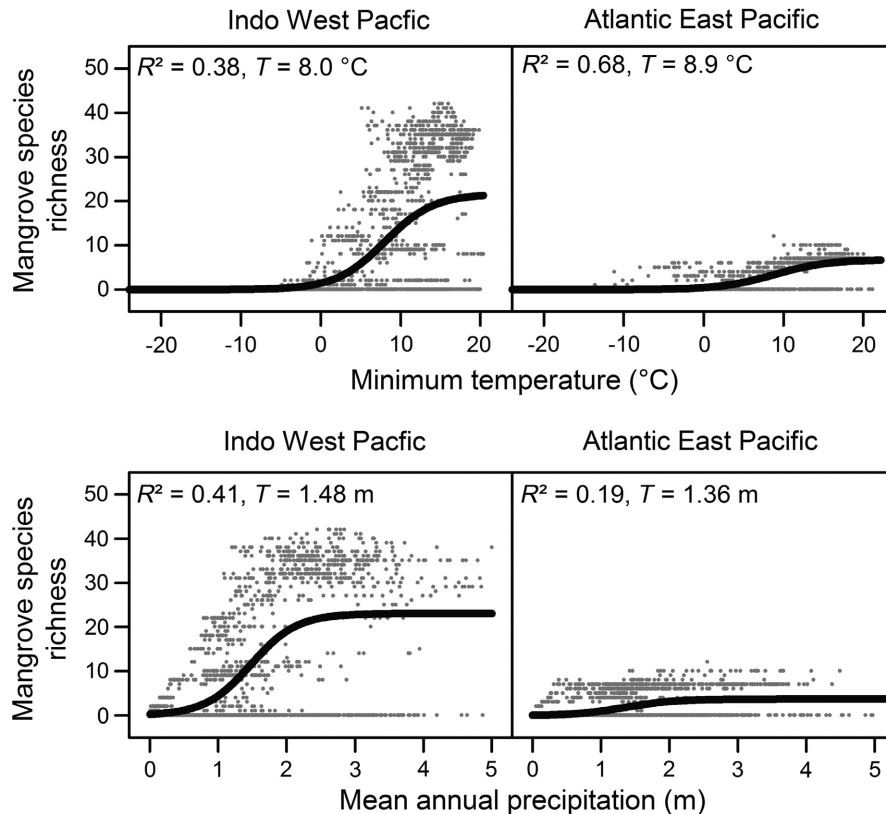
Fig. 4. The relationships between mangrove plant species richness and minimum air temperatures (upper panels) and mangrove plant species richness and mean annual precipitation (lower panels) within two biogeographic zones (Indo West Pacific and Atlantic East Pacific). These biogeographic zones are described in Duke et al. (1998). *T* represents the inflection point or threshold.

respectively). Climatic thresholds for mangrove presence were more often lower than thresholds for mangrove abundance and/or richness (14 out of 20 instances; Figs. 7–11).

## DISCUSSION

Mangrove forests are visually striking ecosystems that have captured the curiosity of many tropical ecologists (Davis 1940, Lugo and Snedaker 1974, Tomlinson 1986, Woodroffe and Grindrod 1991). As a result, the mangrove literature is rich with astute observations and hypotheses regarding the influence of climatic drivers upon mangrove forests (Table 1). In this study, we used recently available climate and ecological data to test some of these hypotheses and improve our understanding of the influence of temperature and rainfall regimes upon the global distribution, abundance, and species richness of mangrove forests. A summary of the range-limit-specific data analyses that were conducted is provided in Appendix S2. Some analyses were deemed inappropriate due to the presence of correlated climatic gradients and/or inappropriate hypotheses. Within 13 of the 14 range-limit regions, there was a correlation between minimum air temperature and mean annual precipitation. In Appendix S3, we provide a detailed discussion of our

designation of appropriate or inappropriate range-limit-specific analyses. The temperature–precipitation correlations within each range limit region are discussed in Appendix S3 and illustrated in Appendix S4.

### Beyond just sea temperatures: air temperature and rainfall regimes are more directly relevant

In the mangrove literature, sea temperature isotherms are often used to describe the global distribution of mangrove forests without mention of the role of air temperature and/or precipitation regimes. Duke (1992) noted that the winter position of the 20°C sea surface temperature isotherm corresponds closely with the global distribution of mangrove forests (see also, Tomlinson 1986, Duke et al. 1998). This correlation is indeed important and noteworthy; however, the role of sea surface temperatures is often discussed in isolation without including the importance of concomitant variation in air temperature and rainfall regimes. Mangrove ecologists from different regions of the world have described the direct role of temperature and precipitation regimes in controlling mangrove range limits (see references in Table 1). Our analyses provide regional-scale quantitative support for those perceptive statements. We contend that although sea surface temperatures are important and
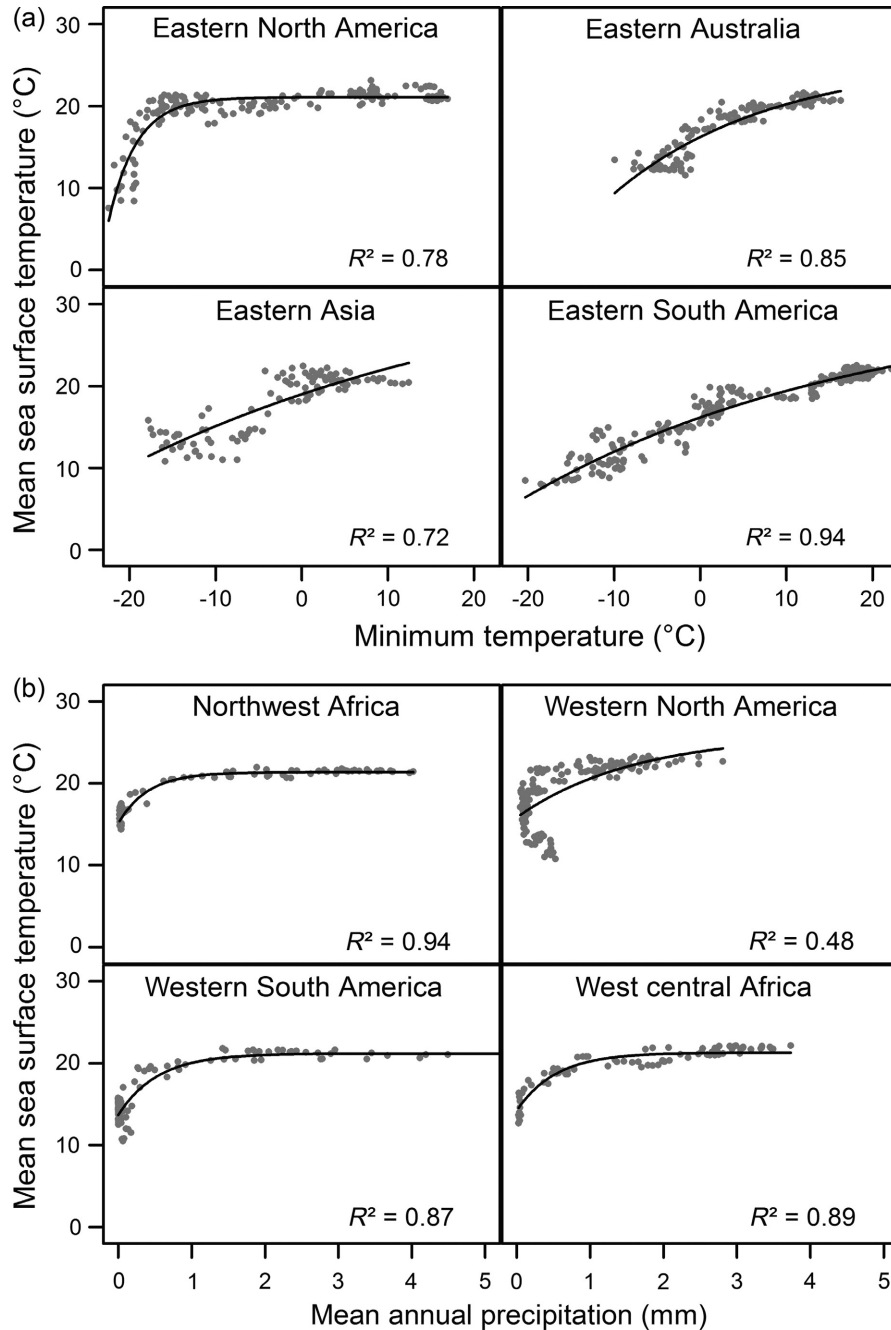
FIG. 5. The range-limit-specific relationships between (a) minimum air temperature and mean annual sea surface temperature and (b) mean annual precipitation and mean sea surface temperature.

may affect certain physiological processes, using sea surface temperatures alone to describe the global distribution of mangroves conceals the important, ubiquitous, and more direct physiological roles of air temperature and rainfall regimes. Here we show that sea surface temperatures are correlated to (1) winter air temperature minima within range limits that are governed by air temperatures and (2) rainfall within range limits that are governed by precipitation (Fig. 5). Note that many of these

relationships have an asymptote near the 20°C sea surface temperature isotherm and that the start of those asymptotes are relatively close to the range-specific climatic thresholds identified here. There is no doubt that sea temperatures play an important role and affect mangroves by modulating air temperatures, soil temperatures, and rainfall regimes. The range-limit-specific correlations between sea surface temperatures and minimum temperature or mean annual precipitation are striking (Fig. 5).

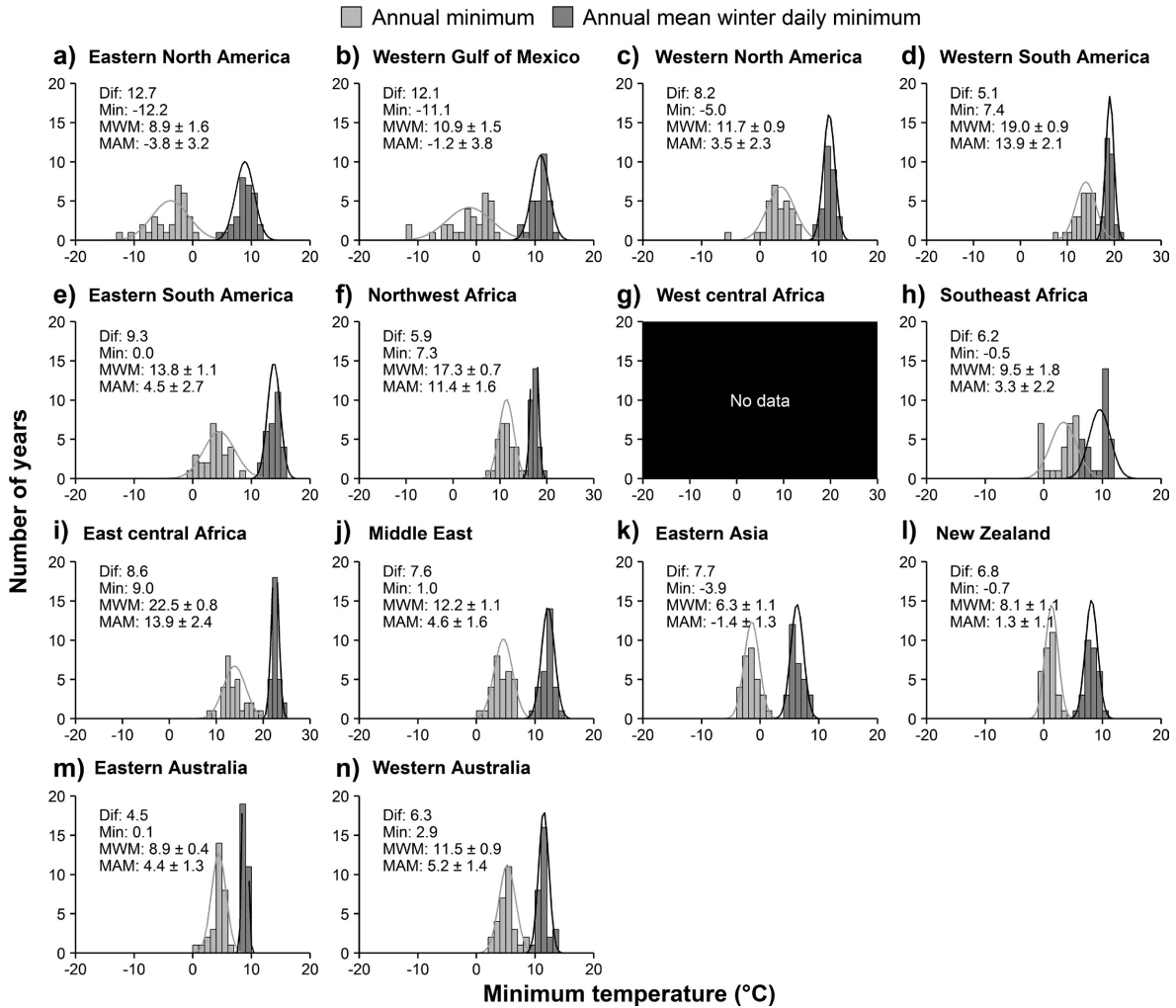☐ Annual minimum   ■ Annual mean winter daily minimum



Fig. 6. Station-based characterizations of typical and extreme winter air temperatures for 13 of the 14 mangrove distributional range limits for a 30-yr period (1981–2010). Dif represents the difference between an extreme annual event and a typical winter minimum (i.e., the difference between the mean annual minimum and the mean annual mean winter daily minimum). Min represents the coldest temperature recorded during the 30-yr period. MWM represents the mean annual mean winter daily minimum temperature. MAM represents the mean annual minimum temperature.

However, from a physiological perspective, winter air temperature and rainfall regimes are more directly relevant climatic variables in many range limits (Lot-Helgueras et al. 1975, Lugo and Patterson-Zucca 1977, Saenger 2002, Méndez-Alonzo et al. 2008, Ross et al. 2009, Lovelock et al. 2016). Although sea surface temperature may be a valuable global-scale surrogate variable under some situations, direct consideration and investigation of the role of air temperatures and rainfall regimes will improve our mechanistic understanding of mangrove
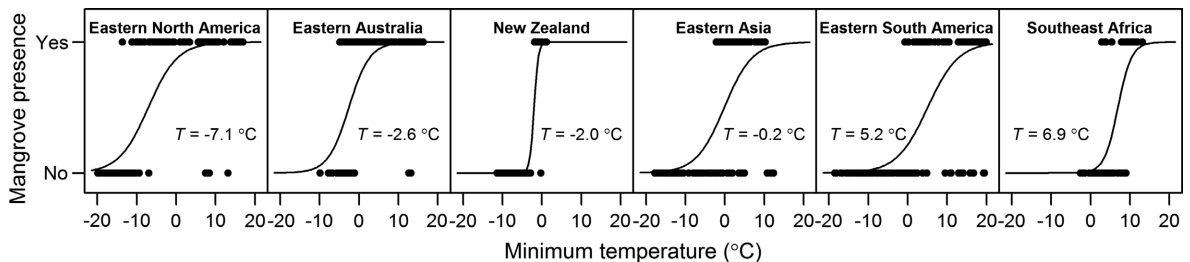


Fig. 7. The range-limit-specific relationships between mangrove presence and minimum air temperatures. $T$ represents the inflection point or threshold.
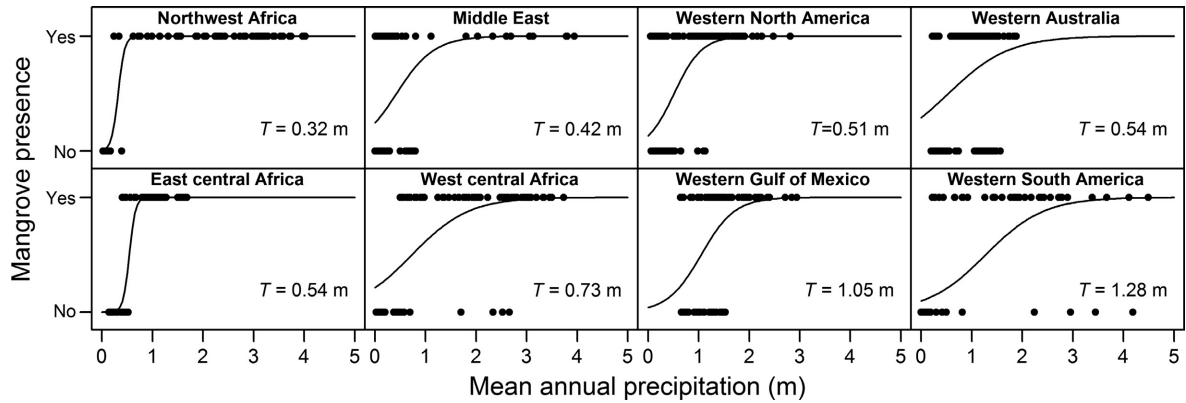
FIG. 8. The range-limit-specific relationships between mangrove presence and mean annual precipitation. *T* represents the inflection point or threshold.
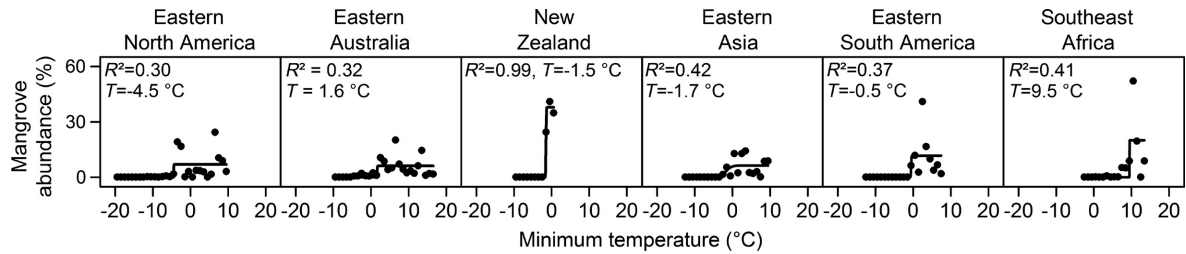


FIG. 9. The range-limit-specific relationships between mangrove abundance and minimum air temperatures. *T* represents the inflection point or threshold.
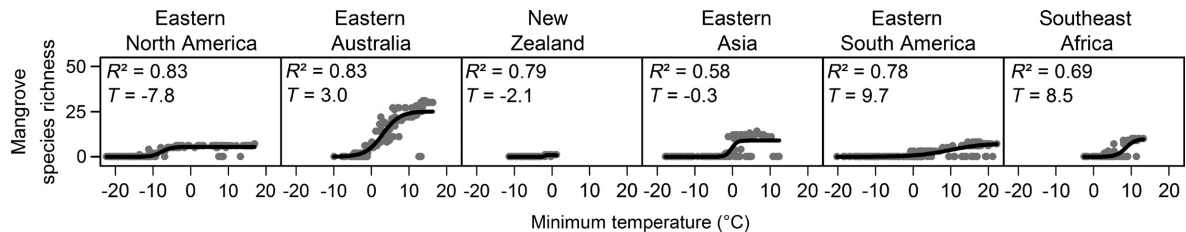


FIG. 10. The range-limit-specific relationships between mangrove plant species richness and minimum air temperatures. *T* represents the inflection point or threshold.

responses to climate change. Rather than focusing solely on sea temperatures, we recommend that discussions of the drivers of the global distribution, structure, and diversity of mangrove forests should also highlight and better elucidate the important and direct role of winter air temperature and rainfall regimes.

*The role of winter air temperature extremes*

Mangrove ecologists have long recognized the importance of winter air temperature regimes (Davis 1940, Chapman 1975, West 1977, Smith and Duke 1987, Woodroffe and Grindrod 1991, Saenger 2002). All mangrove species are sensitive to some level of chilling and/or freezing stress, which can result in reduced metabolic rates, reduced reproductive success, reduced growth, loss of aboveground biomass, and, in extreme cases, mortality (Stuart et al. 2007, Ross et al. 2009, Lovelock et al. 2016). Because relevant air temperature data have historically been difficult to obtain across large spatial scales, many of the initial global- and regional-scale analyses of the influence of air temperature used latitude as a surrogate variable (reviewed by Alongi 2009, Twilley and Day 2012). For example, Duke (1990*b*) characterized the relationships between latitude, air temperatures, and reproductive success. Twilley et al. (1992) showed that there was a negative relationship between latitude and mangrove abundance, biomass, productivity, and carbon storage. Saenger and Snedaker (1993) quantified the negative relationship between latitude and mangrove
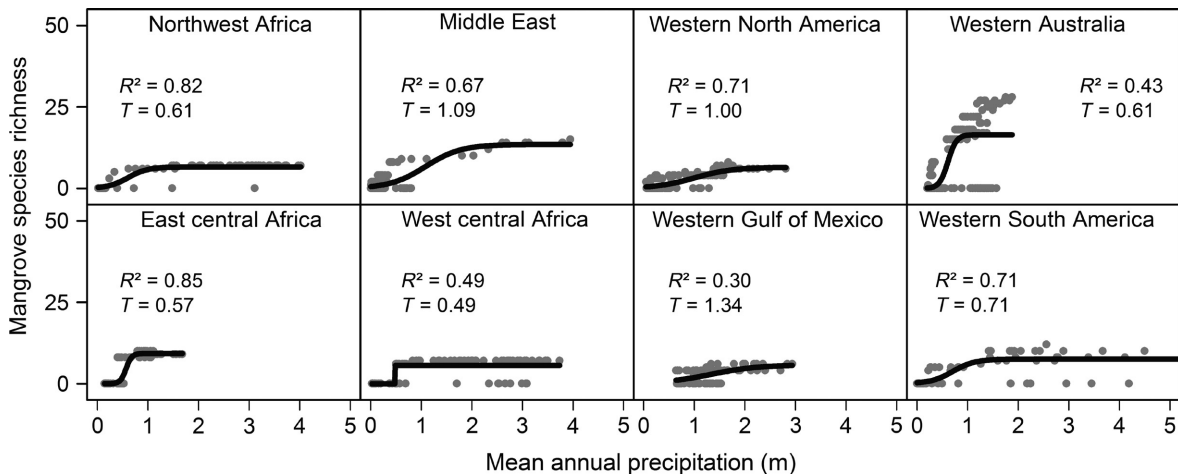
FIG. 11. The range-limit-specific relationships between mangrove plant species richness and mean annual precipitation. *T* represents the inflection point or threshold.

biomass and productivity. Ellison (2002) identified a negative relationship between latitude and mangrove plant species richness, and Bouillon et al. (2008) used additional data to update the relationship between latitude and productivity. Collectively, these examples reflect a long history in the literature of using latitude as a surrogate for air temperature.

In the last several years, the quality and accessibility of global-scale air temperature and ecological data have been improving, which has provided opportunities to better quantify climate-mangrove linkages. At the global scale, there have been several recent studies that have directly included air temperature regimes in models of mangrove distribution (Quisthoudt et al. 2012, Record et al. 2013), biomass (Hutchison et al. 2014, Rovai et al. 2016), and soil carbon stocks (Jardine and Siikamäki 2014). All of these studies show that air temperatures are important; however, global-scale data of air temperature extremes are currently more difficult to obtain than data of monthly mean temperatures (Donat et al. 2013), and all of these studies utilize temperature variables based upon means (e.g., monthly means) rather than extremes (e.g., temperature associated with extreme freeze events; absolute minimum air temperatures).

Our analyses of station-based data near range limits across the world (Fig. 6) illustrate the importance of considering extremes rather than just means for understanding mangrove range limitation. These station-based analyses provide us with an estimate of relevant minimum temperature thresholds within each range limit (i.e., the Min in each panel of Fig. 6) and they also highlight differences between extreme and mean temperatures. In some range limits (e.g., eastern North America, western Gulf of Mexico, and eastern Asia), the differences between typical and extreme winter temperatures are especially large (i.e., the Dif in Fig. 6a, b, k). In other range limits (e.g., eastern Australia, New Zealand), the differences between means and extremes are lower. Such

differences in the role of extremes vs. means can affect mangrove plant traits and physiological processes (e.g., xylem diameter, vascular embolism, water transport, growth rates, vulnerability to freezing; Markley et al. 1982, Madrid et al. 2014, Cook-Patton et al. 2015). For example, in a comparison of *Avicennia* species from North America and Australia (*A. germinans* and *A. marina*, respectively), Stuart et al. (2007) hypothesized that, despite colder extremes in North America, the typically mild winters in the region result in larger xylem vessel diameters, more rapid growth, and earlier reproduction; in contrast, the consistently cooler, but less extreme, typical winters in Australia result in smaller xylem vessel diameters, slower growth, and low reproduction success (see also Duke 1990b).

Using data for eastern North America, several recent studies have quantified the importance of winter air temperature extremes in governing regional-scale mangrove distribution and structure (Osland et al. 2013, 2015, 2016, 2017, Cavanaugh et al. 2014, 2015; Gabler et al., 2017). These studies have demonstrated the potential to identify ecological thresholds via analyses that incorporate variables based upon absolute minimum air temperatures. From a physiological perspective, winter air temperature extremes can be very important for mangroves, and we recommend that, where appropriate and feasible, global-scale models of mangrove structure and function should incorporate air temperature variables that are reflective of minimum temperatures associated with extreme freezing and/or chilling events that may occur only once every few years or decades. Our station-based analyses show that the amount of time needed to characterize these extremes (i.e., years or decades) is range limit specific.

To characterize the role of temperature extremes in this study, we used the absolute minimum daily air temperature (i.e., the coldest daily air temperature that occurred across a recent multi-decadal period), which has been

identified as a valuable metric for identifying regional-scale thresholds (Osland et al. 2013, 2016, 2017). At the global scale, we identified a sigmoidal relationship between minimum temperature and mangrove abundance. Within the two biogeographic zones (i.e., IWP and AEP), we identified similar relationships between minimum temperature and mangrove plant species richness. Despite these highly significant global relationships, the global-scale thresholds were not as meaningful at the range limit scale due to range-limit-dependent differences in winter temperature regimes and the role of extremes (e.g., the differences noted in Fig. 6). Hence, our most meaningful results are from the range-limit-specific analyses. Based on the literature, we identified 10 range limits where we expected that winter temperatures affect mangroves (Table 1). In four of these ten range limits (i.e., eastern North America, eastern Australia, New Zealand, and eastern Asia), we identified minimum temperature-based ecological thresholds. Eastern North America stands out as having the coldest thresholds, in the world, for mangrove presence, abundance, and richness. At the eastern North America range limit, typical winter air temperatures are relatively mild; however, the extreme freeze events that occur in eastern North America are much colder than any other mangrove range limit (Fig. 6). The threshold in eastern North America for mangrove presence was at least 4.5°C colder than those identified for eastern Australia, New Zealand, and eastern Asia.

Based on known physiological tolerances of mangrove species, the identified temperature thresholds in 2 of the 10 temperature-affected range limits (i.e., eastern South America and southeast Africa) were higher than expected, and we suspect that mangroves in these regions are not at their physiological temperature limit, perhaps due to dispersal limitations and/or habitat availability constraints (i.e., lack of available habitat for mangrove establishment beyond and near their current southern range limit; Schaeffer-Novelli et al. 1990, Adams et al. 2004, Soares et al. 2012, Quisthoudt et al. 2013, Ximenes et al. 2016; Naidoo, 2016). We presume that the physiological thresholds for mangrove presence, abundance, and richness in these two range limits are likely lower than identified here. In eastern Australia, the southern limit of mangroves is also constrained by dispersal limitations as easterly currents through Bass Strait prevent propagules from reaching Tasmania (Saintilan et al. 2014). Hence, it is possible that the physiological temperature thresholds for *A. marina* individuals near the eastern Australian range limit are also lower than identified in our analyses. Quisthoudt et al. (2012) and Saintilan et al. (2014) provide valuable discussions of partial range filing that is caused by dispersal constraints and lack of available habitat.

Of the nine range limits where we hypothesized that temperature is an important climatic driver (Table 1), there are interesting differences between limits in the northern and southern hemispheres. As mentioned, dispersal constraints and lack of potential habitat are particularly common in the southern range limits. Several southern hemisphere range limits occur on wave-dominated coasts where intermittently closed estuary entrances (Roy et al. 2001, Haines et al. 2006) greatly influence mangrove dispersal and performance. For example, in eastern Australia and southeast Africa, the closure of estuary entrances can prevent mangrove propagule entrance or result in mangrove mortality after closure due to inappropriate hydrologic regimes (Rajkaran et al. 2009, Quisthoudt et al. 2013). In general, temperature extremes in the northern hemisphere range limits (i.e., eastern North America, western Gulf of Mexico, western North America, and East Asia) are colder than in the southern hemisphere (i.e., New Zealand, eastern Australia, western Australia, and eastern South America) (Fig. 6). Near northern hemisphere range limits, mangroves can be affected by cold polar air, which travels across land in North America or Asia. In contrast, range limits in the southern hemisphere are buffered by large expanses of ocean that lessen the intensity of extremes.

In four range limits (i.e., western Gulf of Mexico, western North America, Middle East, and western Australia), we expect that precipitation and minimum air temperatures both affect mangrove distribution, abundance, and species richness. This expectation is based on (1) our literature review (i.e., the references in Table 1 for these range limits), (2) our analyses of the gridded and station-based climate data, and (3) the identified mangrove physiological thresholds from other range limits. The literature from these four range limits contains reports of mangrove stress due to hypersaline conditions and/or freezing temperatures (Table 1). The station-based data for these four range limits (Fig. 6) indicate that air temperature extremes are low enough to cause freezing and/or chilling stress. In all four of these range limits, we were able to identify ecologically meaningful precipitation thresholds because low rainfall precedes low temperatures. Moving in a poleward direction in all four of these range limits, low precipitation begins to affect mangroves before low temperatures. These concomitant gradients prevented us from quantifying temperature–mangrove relationships and thresholds. We suspect that, for these four range limits, low rainfall and hypersaline conditions are more regionally important climatic drivers than winter temperature regimes. However, low temperatures play an important role in certain portions of each of these four range limits. In areas where local hydrologic factors lead to local reductions in salinity, minimum temperatures would be expected to influence mangrove presence and abundance. For example, this scenario occurs near tidal inlets of the Laguna Madre system of the western Gulf of Mexico (Sherrod and McMillan 1981) and areas with local groundwater inputs in northwestern Australia (Semeniuk 1983). The station-based minimum temperatures from these range limits (i.e., the Min values in Fig. 6) in combination with observations from the literature (Table 1)

can be used to estimate temperature thresholds within these four range limits.

Since mangroves can establish and persist in physically stressful environments before they become abundant or species rich, we expected that temperature-based thresholds would be lower for mangrove presence than for abundance and/or species richness (Fig. 1). However, this pattern was not always reflected in our results. While the identified temperature-based thresholds for presence, abundance, and richness were relatively close within range limits, there were five cases out of 12 where the range-limit-specific threshold for abundance or species richness was higher than for presence. We expect that this variation is likely due to poor data resolution in certain regions, and we anticipate that future analyses will be improved by better climate and ecological data. The Giri et al. (2011) and Spalding et al. (2010) mangrove distribution data sets only capture relatively dense stands of mangroves; presence of individual mangrove plants beyond the range of abundant populations is simply unknown or not mapped in many areas. In addition to improvements from higher-resolution mangrove data, we expect that future analyses will benefit from the incorporation of a potential tidal saline wetland habitat metric (sensu Osland et al. 2013, 2014). The ability to quantify the total tidal saline wetland coverage (i.e., salt marshes, mangrove forests, and salt flats, collectively) as well as the coverage of these individual habitats would greatly improve our ability to characterize the ecological role of climatic drivers. For example, in the southeastern United States, Osland et al. (2013) was able to identify mangrove dominance thresholds by quantifying the relative contribution of salt marsh and mangrove forests to the total tidal saline wetland area within a cell. Similarly, in the northwestern Gulf of Mexico, Osland et al. (2014) used salt flat and vegetated wetland data together to quantify precipitation-based thresholds for wetland plant coverage. In the future, we expect that the analyses presented here will be greatly improved via the incorporation of global-scale mangrove, salt marsh, salt flat, and total tidal saline wetland area data. Higher resolution and more spatially consistent minimum air temperature data will also augment these analyses.

Our presence and abundance analyses group all mangrove species into a single mangrove forest category. However, we know that there is tremendous species-specific variation in sensitivity to freezing and/or chilling (Clough 1992, Lovelock et al. 2016). For example, in eastern North America and the rest of the AEP biogeographic zone, *A. germinans* is more freeze-tolerant than *R. mangle* and *L. racemosa* (Ross et al. 2009, Day et al. 2013, Cavanaugh et al. 2015). In the IWP biogeographic zone, *A. marina* and *Kandelia obovata* are among the most freeze-tolerant species. The temperature thresholds for these freeze-tolerant species would be much lower than for tropical mangrove species that are sensitive to chilling stress (e.g., *Lumnitzera littorea*, *Nypa fruticans*, *R. apiculata*; Lovelock et al. 2016). Species-specific

thresholds could likely be quantified and compared using the Polidoro et al. (2010) mangrove species distribution data. In addition to inter-species specific variation, intra-species specific variation is also known to be important (Tomlinson 1986, Duke 1990*a*); individuals from different climatic regimes possess different plant traits and physiological adaptations for freeze tolerance (McMillan and Sherrod 1986, Stuart et al. 2007, Madrid et al. 2014, Cook-Patton et al. 2015).

### *The role of precipitation*

In terrestrial ecosystems, rainfall governs many ecological transitions between biomes and ecosystems (e.g., transitions between terrestrial forested, grasslands, and desert ecosystems) (Holdridge 1967, Whittaker 1970, Staver et al. 2011). Rainfall plays a similarly important role in mangrove forests and other coastal wetlands. Lack of rainfall and freshwater inputs can lead to the accumulation of oceanic salts and the development of hypersaline conditions, which are physiologically stressful to mangroves and other tidal saline wetland plants (Ball 1988, Diop et al. 1997, Eslami-Andargoli et al. 2009, Reef and Lovelock 2014, Lovelock et al. 2016). Hypersaline conditions that exceed mangrove plant physiological thresholds are especially common along arid and semiarid coasts, and mangrove ecologists have long noted the influence of low rainfall and high salinity upon mangrove forest distribution, abundance, and species richness (Davis 1940, Cintrón et al. 1978, Semeniuk 1983, 2013, Saintilan et al. 2009, Asbridge et al. 2015). Saenger (2002) and Spalding et al. (2010) provide detailed global-scale observations regarding the influence of rainfall on mangrove biogeography. Bucher and Saenger (1994) quantified the relationship between mean annual rainfall and mangrove abundance in Australia. In the northwestern Gulf of Mexico, there is also a strong relationship between rainfall and the abundance of tidal saline wetland plants (i.e., salt marsh and mangrove plants; Longley 1994, Montagna et al. 2007, Osland et al. 2014, 2016; Gabler et al., 2017). In general, as rainfall and freshwater inputs decrease, salinities increase and salt flats (i.e., hypersaline areas without plant coverage) become more abundant. In the last several years, precipitation has been included in global-scale models of mangrove biomass (Hutchison et al. 2014, Rovai et al. 2016), distribution (Record et al. 2013), and soil carbon (Jardine and Siikamäki 2014). All of these studies show that precipitation plays an important role at the global scale for these ecological attributes.

With regard to the role of precipitation, our aim in this study was to quantify the influence of rainfall on the distribution, abundance, and species richness of mangrove forests at global and range-limit-specific scales. At the global scale, we show that rainfall controls the abundance of mangrove forests. We identify a sigmoidal relationship between annual precipitation and the abundance of mangrove forests. The global-scale precipitation-based

threshold for mangrove abundance was 0.78 m rainfall per year. Within the two biogeographic zones (i.e., IWP and AEP), we identified a sigmoidal relationship between precipitation and mangrove plant species richness. The precipitation-based species richness thresholds within these two biogeographic zones were 1.48 and 1.36 m rainfall per year, respectively. We identified eight range limits where, based on information in the literature, we expected that precipitation gradients play an important role. We characterized the relationships between precipitation and mangrove presence or species richness within each of these eight range limits. The range-limit-specific precipitation-based thresholds for mangrove presence and species richness ranged from 0.32 to 1.34 m of rainfall per year. The variation in these range-limit-dependent thresholds is likely influenced by many factors and processes including topography, seasonality of rainfall inputs, tidal connectivity, tidal range, temperature, evapotranspiration, and, importantly, the spatial and temporal distribution of ground and surface freshwater inputs. The range-limit-specific thresholds correspond fairly well with the global-scale thresholds identified here as well as results and observations from previous studies (e.g., Semeniuk 1983, Bucher and Saenger 1994, Longley 1994, Montagna et al. 2007, Osland et al. 2014; Gabler et al., 2017). We hypothesized that precipitation-based thresholds would be lower for mangrove presence than for abundance and/or species richness (Fig. 1), and this pattern was present in six of the eight range limits. The absence of this pattern in certain areas is likely due to poor climate and/or mangrove data resolution. Global-scale climate and ecological data are improving rapidly, and we expect that our analyses will be improved in the near future.

## Conclusions and climate change implications

Due to their position at the land-sea interface, mangrove forests are sensitive to many different aspects of climate change (Woodroffe and Grindrod 1991, McKee et al. 2012, Saintilan et al. 2014, Alongi 2015, Asbridge et al. 2015, Ward et al. 2016). Although ecologists have long recognized that temperature and rainfall regimes control the global distribution, abundance, and species richness of mangrove forests, these relationships have not been well quantified at the global scale due primarily to data constraints. In this study, we used the best available data to quantify climate–mangrove linkages at the global scale as well as within 14 regions that contained a mangrove range limit. Our findings provide quantitative support for the insightful observations provided by earlier mangrove ecologists working in different regions of the world (i.e., our analyses support the hypotheses presented in Table 1). Our global analyses reveal strong linkages between climatic drivers and mangrove distribution, abundance, and species richness. However, our most interesting and meaningful results are from the range-limit-specific analyses. Climatic thresholds for mangrove presence, abundance, and species richness were range-limit specific. These thresholds and relationships provide a foundation for better understanding the effects of climate change on mangrove forests. Our results identify regions of the world where the distribution, abundance, and species richness of mangrove forests are likely to be affected by climate change (Fig. 12). In general, warmer winter temperatures are expected to allow mangroves to expand poleward in wetter regions of the world. However, dispersal and habitat availability constraints may hinder expansion near certain range



T: Warmer winter temperatures lead to mangrove expansion

P: Changes in precipitation lead to mangrove expansion and/or contraction
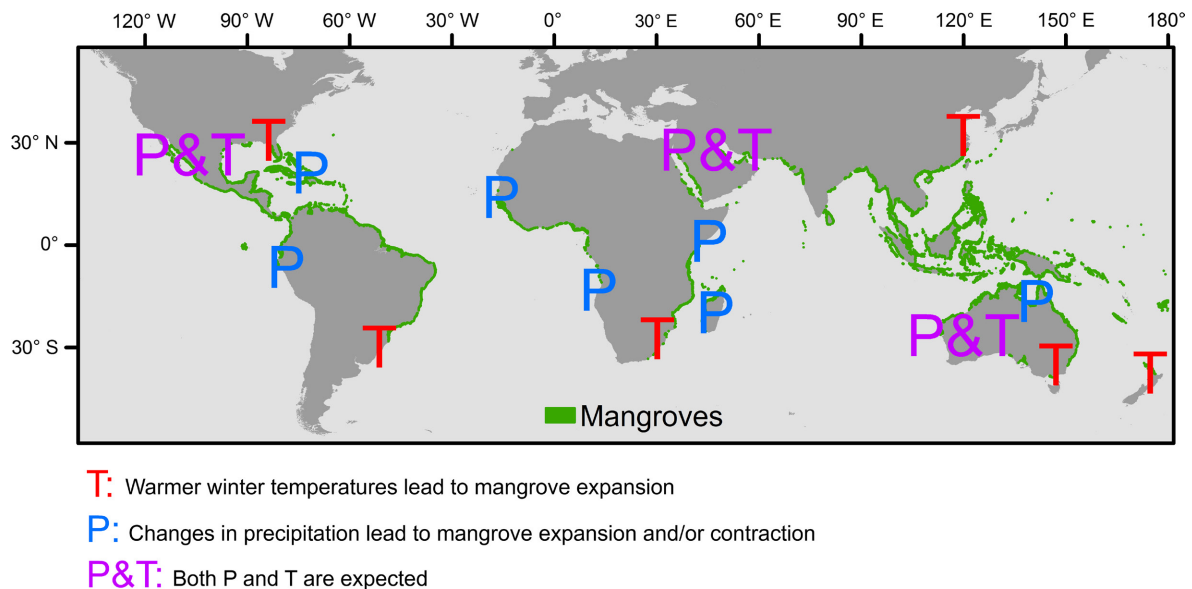
P&T: Both P and T are expected

FIG. 12. Regions where the distribution, abundance, and species richness of mangrove forests are likely to be affected by climate change (specifically, changing air temperature and rainfall regimes).

limits (e.g., eastern South America, southeast Africa, eastern Australia). Along arid and semiarid coastlines, decreases and/or increases in freshwater availability are expected to lead to mangrove contraction or expansion, respectively. Collectively, our analyses improve our understanding of the influence of climatic drivers and climate change upon the distribution, abundance, and species richness of mangrove forests.

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## Supporting Information

## Data Availability