4-28-2017

Sensitivity of mangrove range limits to climate variability

Kyle C. Cavanaugh
Department of Geography, University of California, kcavanaugh@geog.ucla.edu

Michael J. Osland
U.S. Geological Survey, Wetland and Aquatic Research Center

Remi Bardou
Department of Geography, University of California

Gustavo Hinojosa-Arango
Academia de Biodiversidad, Centro Interdisciplinario de Investigacion para el Desarrollo Integral Regional Unidad Oaxaca (CIIDIR-IPN)

Juan M. Lopez-Vivas
Programa de Investigacion en Botanica Marina, Departamento Academico de Ciencias Marinas y Costeras, Universidad

See next page for additional authors

Authors

Kyle C. Cavanaugh, Michael J. Osland, Remi Bardou, Gustavo Hinojosa-Arango, Juan M. Lopez-Vivas, John
D. Parker, and Andre S. Rovai

RESEARCH PAPER

Sensitivity of mangrove range limits to climate variability

Kyle C. Cavanaugh[1] [iD] | Michael J. Osland[2] | Rémi Bardou[1] |
Gustavo Hinojosa-Arango[3] | Juan M. López-Vivas[4] | John D. Parker[5] |
André S. Rovai[6,7]

[1]Department of Geography, University of California, Los Angeles, Los Angeles, California

[2]U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, Louisiana

[3]Academia de Biodiversidad, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Oaxaca (CIIDIR-IPN), Santa Cruz Xoxocotlán, Oaxaca, México

[4]Programa de Investigación en Botánica Marina, Departamento Académico de Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México

[5]Smithsonian Environmental Research Center, Smithsonian Institution, Edgewater, Maryland

[6]Department of Oceanography and Coastal Sciences, College of the Coast and Environment, Louisiana State University, Baton Rouge, Louisiana

[7]Programa de Pós-Graduação em Oceanografia, Centro de Filosofia e Ciências Humanas, Florianópolis, Santa Catarina, Brazil

Correspondence
Kyle C. Cavanaugh, Department of Geography, 1255 Bunche Hall, University of California, Los Angeles, 90095.
Email: kcavanaugh@geog.ucla.edu

Abstract

Aim: Correlative distribution models have been used to identify potential climatic controls of mangrove range limits, but there is still uncertainty about the relative importance of these factors across different regions. To provide insights into the strength of climatic control of different mangrove range limits, we tested whether temporal variability in mangrove abundance increases near range limits and whether this variability is correlated with climatic factors thought to control large-scale mangrove distributions.

Location: North and South America.

Time period: 1984–2011.

Major taxa studied: *Avicennia germinans, Avicennia schuaeriana, Rhizophora mangle, Laguncularia racemosa.*

Methods: We characterized temporal variability in the enhanced vegetation index (EVI) at mangrove range limits using Landsat satellite imagery collected between 1984–2011. We characterized greening trends at each range limit, examined variability in EVI along latitudinal gradients near each range limit, and assessed correlations between changes in EVI and temperature and precipitation.

Results: Spatial variability in mean EVI was generally correlated with temperature and precipitation, but the relationships were region specific. Greening trends were most pronounced at range limits in eastern North America. In these regions variability in EVI increased toward the range limit and was sensitive to climatic factors. In contrast, EVI at range limits on the Pacific coast of North America and both coasts of South America was relatively stable and less sensitive to climatic variability.

Main conclusions: Our results suggest that range limits in eastern North America are strongly controlled by climate factors. Mangrove expansion in response to future warming is expected to be rapid in regions that are highly sensitive to climate variability (e.g. eastern North America), but the response in other range limits (e.g. South America) is likely to be more complex and modulated by additional factors such as dispersal limitation, habitat constraints, and/or changing climatic means rather than just extremes.

KEYWORDS
climatic drivers, distribution, EVI, Landsat, mangrove forests, range limit

1 | INTRODUCTION

Climate change, particularly global increases in temperature, have already led to poleward shifts in the distributions of many species (Parmesan & Yohe, 2003), with especially apparent impacts at the boundaries of major biomes. For example, shrubs and trees have expanded northward in tundra ecosystems across the Arctic in response to recent warming (Tape, Sturm, & Racine, 2006). Similarly, in marine ecosystems around the world tropical herbivores have expanded their range into temperate waters, leading to a loss of habitat-forming species and dramatic community phase shifts (Vergés et al., 2014). These range shifts can have large impacts on the structure and functioning of ecosystems, pointing to a need to better understand the processes that control species' range limits.

Correlative distribution modelling has become one of the most common approaches for gaining insight into the processes that control species' distributions and for predicting changes to those distributions (Elith & Leathwick, 2009). These types of models are based on the statistical association between species occurrences and environmental or climate data. These models are flexible in that they utilize readily available data and are relatively simple to implement. However, correlative distribution models assume that a species is in equilibrium with its environment, which may not be the case during rapid climate change or when a range limit is controlled by dispersal limitation or biotic interactions (Kearney & Porter, 2009).

Data on the temporal fluctuations in abundance or performance of a species near its range limit can provide additional insight into the processes that control its distribution, and thus be used to test predictions of correlative distribution models. If a range limit is controlled by an abiotic environmental or climatic factor, then we would expect temporal variability in that factor to correlate with variability of range limit populations. More generally, if a range limit is set by climatic factors, then population abundance or performance at the range edge, where the species is predicted to be at or near its physiological tolerance limits, should show high temporal variability as environmental fluctuations exceed the species' tolerance in some years (Figure 1A; Sexton, McIntyre, Angert, & Rice, 2009). Alternatively, if a range limit is set by a biotic process such as competition, predation, or dispersal limitation, then edge populations might not be near their environmental tolerance limits, and thus exhibit relatively little temporal variability in population dynamics (Figure 1B). Temporal variability in population dynamics may also be low if variability in the limiting climatic factor is low (Figure 1C). Trends in abundance or performance at range limits might also indicate that a species is not in equilibrium with its environment, and thus be used to identify shifting distributions. Thus, temporal-variability modelling can complement spatial distribution modelling by providing an independent test of the hypothesis that range limits are set by gradients in climatic drivers.

In this study, we examined the relationships between patterns of variability in mangrove abundance and climatic factors thought to control the range limits of mangroves. Mangroves are tropical and subtropical coastal forested wetlands that provide a range of important ecosystem services including habitat for commercially important
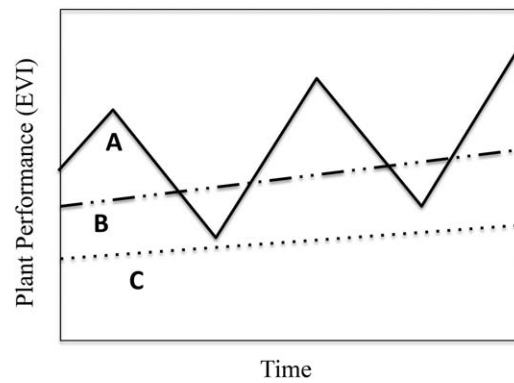

FIGURE 1 Conceptual diagram of enhanced vegetation index (EVI) patterns near different types of range limits. A: Range limit is near climatic tolerance with high climatic variation and so climatic variability drives variability in plant performance, for example 'USA – Atlantic' in Figure 6. B: Range limit is not yet at climatic tolerance due to dispersal limitation and/or habitat constraints. As a result, plant performance is relatively insensitive to climate variability, for example 'Peru' in Figure 6. C: Range limit is near climatic tolerance with low climatic variation. Plant performance is sensitive to climatic variability, but climatic variability is low, for example 'Mexico – Gulf of California' in Figure 6

fisheries, filtering of sediments and nutrients, elevation maintenance and erosion avoidance, and carbon sequestration and storage (Ewel, Twilley, & Ong, 1998). Mangroves are largely found between the latitudes of c. 30°N and c. 40°S; however the latitude of the poleward range limit varies among regions, as do the climatic conditions at those range limits (Osland, Feher, et al., 2017; Quisthoudt et al., 2012).

Previous work has provided valuable insight into the drivers of mangrove range limitation by comparing current mangrove distributions to climatic variables. These studies range from descriptions of climatic conditions at various poleward range limits (Duke, Ball, & Ellison, 1998; Quisthoudt et al., 2012; Saenger, 2002) to models that relate mangrove distributions (Gabler et al., 2017; Osland, Enwright, Day, & Doyle, 2013; Osland, Enwright, & Stagg, 2014; Osland, Feher, et al., 2017; Record, Charney, Zakaria, & Ellison, 2013) and functioning (Feher et al., 2017) to climate data. These studies have generally identified air/water temperature and rainfall as the factors that control the large-scale distributions of mangroves (Osland et al., 2016). Other studies have linked recent increases in mangrove abundance at range limits with changes in climate (e.g. temperature) and other environmental variables (Armitage, Highfield, Brody, & Louchouarn, 2015; Cavanaugh et al., 2014; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). However, there is still uncertainty about how the relative importance of these climatic factors varies across regions with disparate climates.

Here we examined trends and variability in the enhanced vegetation index (EVI) of mangrove forests near range limits in North and South America. EVI is a normalized ratio of near infrared, red, and blue reflectance bands and is strongly correlated to vegetation photosynthetic activity and leaf area index (Jiang, Huete, Didan, & Miura, 2008), two aspects that are typically strongly related to plant productivity (Webb, Lauenroth, Szarek, & Kinerson, 1983). Numerous studies have used normalized difference vegetation index (NDVI), EVI and other
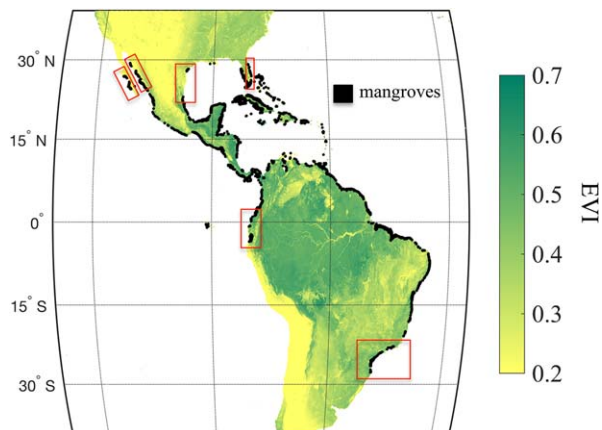
FIGURE 2 Map of the study areas. Red boxes represent each range limit region and extend 5° of latitude from the range limit identified with the Giri et al. (2011) and Spalding et al. (2010) datasets. Colour scale gives the mean enhanced vegetation index (EVI) from 2000–2011. EVI data for this figure were calculated from MODIS Terra imagery. Mangrove distribution data from Giri et al. (2011) and Spalding et al. (2010) [Color figure can be viewed at wileyonlinelibrary.com]

vegetation indices to estimate mangrove extent, density, leaf area index, and canopy closure (Giri, Pengra, Zhu, Singh, & Tieszen, 2007; Green, Mumby, Edwards, Clark, & Ellis, 1997; Kovacs, Wang, & Flores-Verdugo, 2005). We hypothesized that (a) recent mangrove expansion would lead to greening trends in EVI at mangrove range limits, (b) variability in EVI would increase towards range limits, and (c) variability in EVI would be correlated with variation in air temperature and/or precipitation, depending on the specific range limit in question. We expected that range limits on the Atlantic coasts of North and South America would be sensitive to winter air temperature, the range limit on the Pacific coast of South America would be sensitive to annual precipitation, and that range limits on the Pacific, Gulf of California and Gulf of Mexico coasts of North America would be sensitive to both factors. These expectations were based on a study by Osland, Feher, et al. (2017) that examined spatial gradients in temperature and rainfall near various mangrove range limits around the world.

2 | METHODS

2.1 | Study area

Our study area included six mangrove range limits on the Atlantic and Pacific coasts of North and South America (Figure 2): USA – Atlantic (Atlantic coast of North America), USA – northwestern Gulf of Mexico (Gulf coast of North America), Brazil (Atlantic coast of South America), Mexico – Pacific (Pacific coast of North America), Mexico – mainland Gulf of California (Gulf of California coast of North America), and Peru (Pacific coast of South America). There are approximately 14 distinct species of mangroves in the Americas (Spalding, Kainuma, & Collins, 2010), but species richness decreases across temperature and precipitation gradients (Osland, Feher, et al., 2017). Only three to four species are found near mangrove range limits in North and South America. *Avicennia germinans*

(L.) L., *Rhizophora mangle* L. and *Laguncularia racemosa* L. Gaertn. F. are three mangrove species that are present at each of the six range limits we examined (Spalding et al., 2010). These species are the only ones found at the range limits in North America. Another species of *Avicennia* (*Avicennia schuaeriana* Stapf & Leechm. ex Moldenke) can be found in Peru as well as near the range limit in Brazil (Schaeffer-Novelli et al., 1990; Spalding et al., 2010). Coastal wetlands poleward of mangrove range limits are generally dominated by salt marsh or unvegetated tidal flats.

2.2 | Mangrove EVI

We used two global mangrove distribution datasets (Giri, Ochieng, et al., 2011; Spalding et al., 2010) to identify mangrove range limits. The Giri et al. (2011) dataset is a map of global mangrove coverage derived from 30-m resolution Landsat imagery collected around the year 2000. The Spalding et al. (2010) data uses a variety of sources including *in situ* observations, aerial photos and satellite imagery. In order to avoid errors of commission, we limited our analyses to areas identified as mangroves by both of these datasets. Thus, our range limits can be considered as the locations of the most poleward stands of mangroves as opposed to the most poleward individual mangroves. We made one exception to this rule and used the Giri et al. (2011) dataset to identify the mangrove range limit in the western Gulf of Mexico (Texas). Here, the Spalding et al. (2010) dataset omitted an area that is known to contain adult mangrove stands (Armitage et al., 2015; Sherrod & McMillan, 1981). For each range limit (Figure 2), we extracted all mangrove areas within 5 degrees of latitude of the range limit. Restricting our study area in this manner enabled us to examine variability in EVI along a latitudinal gradient, while ensuring that we were analysing the same group of three to four mangrove species as other species generally do not occur within these areas. These species have similar global distributions (Spalding et al., 2010), and so we are considering them an assemblage of species with similar macroclimatic tolerances that can be grouped together for the purposes of modelling climatic sensitivity. Latitude was correlated to the climatic variables of interest (minimum temperature and/or precipitation) for each of the range limit regions (Osland, Feher, et al., 2017).

EVI of mangroves in our study areas was calculated for the period from 1984–2011 using atmospherically corrected surface reflectance data derived from 30-m Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) imagery (Feng et al., 2013). The EVI analysis was performed using Google's Earth Engine, a cloud-based platform for earth observation data analysis (Google Earth Engine Team, 2015). Each Landsat sensor captures an image of a given location every 16 days; however, temporal coverage of our study areas varied due to image availability and cloud cover. The average number of observations per year ranged from four (Peru) to 21 (Mexico – Gulf of California) with a median of 14.

This study assumed that variation in EVI was related to population dynamics near mangrove range limits. Other studies have used similar satellite data to document changes in abundance of mangroves in these regions (Armitage et al., 2015; Cavanaugh et al., 2014; Giri & Long, 2016; López-Medellín et al., 2011), and vegetation indices such as EVI

have been used to identify disturbances leading to mangrove mortality (Zhang, Thapa, Ross, & Gann, 2016). In order to examine the relationship between Landsat EVI and mangrove area, we compared EVI of Landsat pixels to estimates of mangrove cover calculated from 1-m resolution IKONOS imagery for a site near the southern portion of the mangrove–saltmarsh ecotone along the Atlantic coast of Florida (Supporting Information Figure S1). We used the Giri et al. (2011) dataset to identify 16 discrete stands of mangroves. We then compared the mean EVI of the Landsat pixels within each stand to the percent cover of mangroves measured from an unsupervised classification performed on the IKONOS imagery. We found a highly significant relationship between EVI and mangrove percent cover ($R^2 = .69$, $p < .01$; Supporting Information Figure S2).

Landsat pixels (30 m) may contain a mixture of mangroves and other land cover types such as salt marsh. In order to test whether variations in EVI of purported mangrove pixels were actually due to fluctuations in salt marsh greenness, we also examined trends and variability in EVI of salt marshes near each mangrove range limit. There is currently no globally consistent coastal salt marsh distribution dataset available, and so we used Google Earth to manually identify a sample of salt marshes poleward of each mangrove range limit.

2.3 | Climate data

The poleward mangrove range limits in this study spanned a wide range of climatic conditions (Supporting Information Figure S3; Osland, Feher, et al., 2017). We used global gridded air temperature and precipitation data to characterize the climatic conditions at each range limit region. Daily air temperature and precipitation data from 1984–2011 were acquired from a 0.5° resolution global gridded climate dataset provided by the NOAA Climate Prediction Center (data available at https://www.esrl.noaa.gov/psd/data/gridded/) and resampled to 1° cells. Previous studies have documented the importance of temperature extremes, rather than means, in controlling the distribution and abundance of mangroves in North America (Cavanaugh et al., 2014; Osland et al., 2013). As a result, we calculated the temperature of the coldest day of each year in the dataset. To avoid double-counting days in different calendar years but occurring within the same season, a year was defined as the period from December 1 to November 30 for regions in the Northern Hemisphere and from June 1 to May 31 for regions in the Southern Hemisphere. We also calculated mean annual temperature over this time period as it is a variable commonly used in species distribution models. Finally, we calculated the total precipitation for each year in the same fashion.

2.4 | Data analyses

We examined variability in mangrove EVI and climatic variables in 1° bins across a 5° latitudinal gradient at each range limit region. Not all latitudinal bins in each range limit region contained mangroves. Due to Google Earth Engine processing limitations, the 30-m resolution Landsat EVI images were resampled to 150-m resolution prior to further analysis. The amount of mangrove area within each 1° latitudinal bin varied across regions, and so to standardize the area analysed across regions, we randomly sampled one hundred 150-m Landsat cells within each 1° latitudinal bin and calculated the mean EVI of these cells for each available image date. This random sampling was repeated 10,000 times in order to estimate 95% confidence intervals for the EVI time series of each 1° latitudinal bin. We used the climate grid cell closest to the centroid of the mangrove observations to characterize the climate of that bin. All subsequent analyses were performed at the 1° resolution.

We calculated the mean EVI for each year for each region in order to characterize interannual variability in EVI. We used linear regression to summarize the trend in annual mean EVI for each region. Temporal variability in EVI was characterized by calculating the standard deviation in annual mean EVI. We used multiple linear regression to examine the sensitivity of changes in EVI to variability in air temperature and precipitation. We used EVI changes (i.e. $EVI_{t+1} - EVI_t$) for this regression analysis in order to reduce temporal autocorrelation of the data. We normalized the response and predictor variables prior to the analysis in order to estimate the relative importance of each climate variable on annual changes in EVI. Each range limit was analysed separately as climatic thresholds for mangrove presence and abundance have been suggested to be range limit specific (Osland, Feher, et al., 2017).

We also compared the standard deviation in annual EVI to the standard deviation in annual minimum temperature and precipitation across range limits. The goal of this analysis was to examine whether range limits that experienced higher variability in climatic factors were more sensitive to those climate fluctuations.

3 | RESULTS

3.1 | Spatial variability and temporal trends in EVI

Spatial analysis of EVI and climate data indicated that mean EVI increased with increasing minimum temperature and precipitation along most of the latitudinal gradients in our study area (Figure 3). EVI increased with temperature along the Atlantic and Gulf of Mexico coasts of the USA, along the Pacific and Gulf of California coasts of Mexico, and Peru (we did not test the significance of these relationships due to limited sample sizes within regions). EVI increased rapidly with precipitation along latitudinal gradients on the Atlantic and Gulf of Mexico coasts of the USA and the Pacific and Gulf of California coasts of Mexico (Figure 3b). However, because these relationships varied among regions, the overall relationship between EVI and these climate factors was weak.

Mangroves in the southeast USA range limit regions exhibited strong greening trends (i.e. increase in EVI) from 1984–2011 (Figure 4; see slopes in Table 1). This greening signal was especially strong at mangrove range limits on the Atlantic and northwestern Gulf of Mexico coasts of the USA. In these regions, greening was most rapid between 1990 and 2005; after 2005, rates of increase in EVI slowed. Increases in EVI were also present but less pronounced at range limits on the Pacific coast of Mexico and the Atlantic coast of South America. Greening trends were not as prevalent in salt marshes close to the mangrove range limits (Supporting Information Figure S4; Table S1).
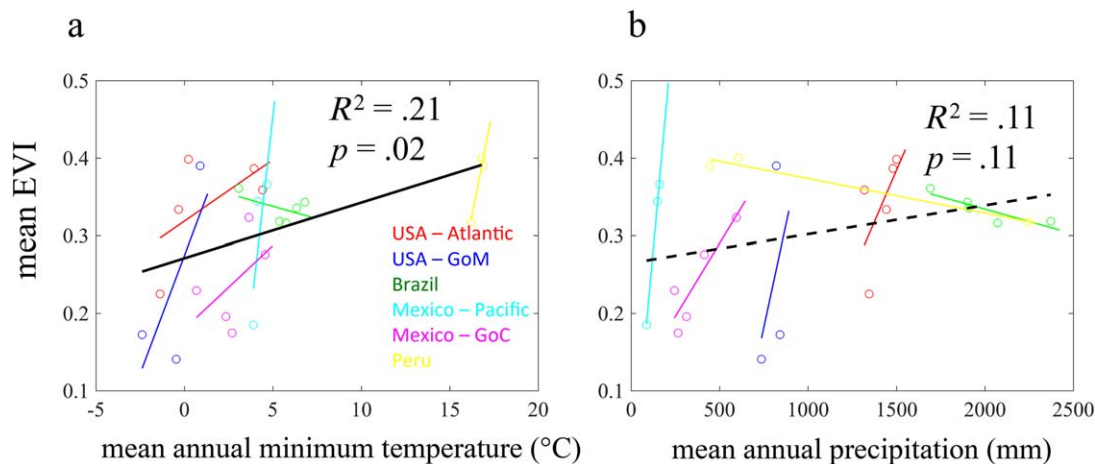
FIGURE 3 Relationships between mean annual enhanced vegetation index (EVI) and (a) mean annual minimum temperature (°C), that is, the average of the coldest day of the year, and (b) mean annual precipitation (mm) from 1985–2011 across study regions. Each point represents a 1° grid cell and cells are coloured by region. Within-region relationships for regions hypothesized to be controlled by minimum temperature and precipitation are given by the coloured lines. The black lines give the overall relationship between the variables. GoC = Gulf of California; GoM = Gulf of Mexico. [Color figure can be viewed at wileyonlinelibrary.com]

3.2 | Temporal variability in EVI

The trend of increasing EVI in the Atlantic USA and northwestern Gulf of Mexico coasts was punctuated by a large decrease in EVI in 1990 (Figure 4). These regions then exhibited relatively rapid greening until 2005–2006. The northwestern Gulf of Mexico range limit experienced a relatively small decline in EVI in 2009 and 2011. There were no major decreases in EVI at the range limit in Brazil. At this range limit, moderate increases in EVI were observed in 1990, 1996 and 2010, but each of these increases was followed by a decrease in EVI during the following year. There were no major disturbances in the EVI time series for the range limits on the Pacific side of the Americas (Figure 4b).
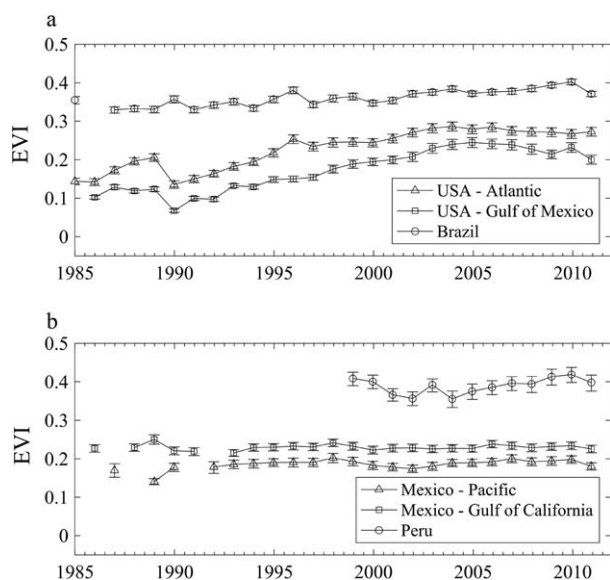
Along the Atlantic and Gulf of Mexico coasts of the USA, interannual variability in EVI increased toward mangrove range limits (Figure 5). In contrast to the Atlantic and Gulf of Mexico coasts of the USA, there did not appear to be any latitudinal pattern in EVI variability along the coasts of Brazil or Peru. Surprisingly, variability in EVI increased away from the range edge for the range limits in Mexico.

3.3 | Sensitivity of EVI to climate variability

A preliminary analysis showed that annual changes in EVI were not significantly correlated to mean annual temperature for any of the range limits. As a result, we removed that variable from our multiple regression analyses, leaving annual minimum temperature and annual precipitation as our climate variables. Annual changes in EVI were significantly correlated with annual minimum temperature for the range limits on the Atlantic and Gulf of Mexico coasts of the USA (Table 2; Supporting Information Figure S6). In both of these regions, the relationship was strongest for latitudinal bins at or near the range limit. Surprisingly, the relationship was negative for the latitudinal bin at 25.5°N, equatorward of the range limit on the Atlantic coast of the USA. On the Gulf of Mexico coast, changes in EVI were also significantly correlated with annual

FIGURE 4 Time series of annual mean enhanced vegetation index (EVI) for range limits on (a) Atlantic and (b) Pacific coasts of North and South America. These time series are from the most poleward 1° grid cell. Error bars represent 95% percent confidence intervals

TABLE 1 Linear trends in mean annual enhanced vegetation index (EVI; 1984–2011) for mangrove range limits. Slopes represent changes in EVI (unitless) per year

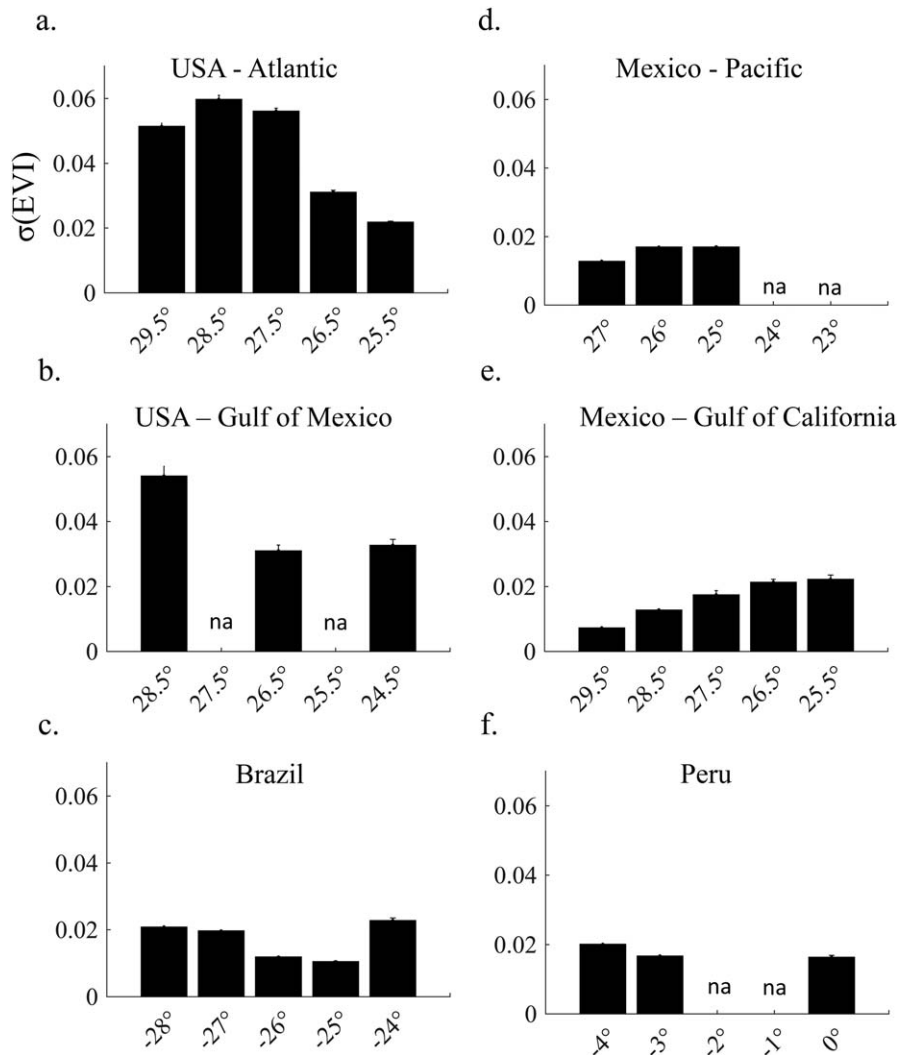| Region	R^2	Slope	p-value
USA – Atlantic	.81	0.006	< .001
USA – Gulf of Mexico	.81	0.007	< .001
Brazil	.67	0.002	< .001
Mexico – Pacific	.28	0.001	.01
Mexico – Gulf of California	.01	0.000	.69
Peru	.15	0.002	.19

FIGURE 5 Standard deviation of mean annual enhanced vegetation index (EVI) for latitudinal gradients around mangrove range limits on Atlantic (a–c) and Pacific (d–f) coasts of North and South America. For each panel, the latitudinal bin on the left side of the plot represents the range limit. Error bars represent 95% percent confidence intervals

precipitation at the range limit. Again, this relationship was weaker for latitudinal bins south of the range limit. In contrast, the strength of the relationship between EVI changes and precipitation increased away from the range limit on the Atlantic coast of the USA. Years with higher precipitation were associated with increases in EVI for all of the latitudinal bins analysed on the Pacific coast of Mexico, but this relationship was not significant. The relationship was significant for two of the latitudinal bins on the Gulf of California coast of Mexico, but there was no discernible trend across the latitudinal gradient. Changes in EVI were not correlated with either minimum temperature or precipitation on the coast of Brazil. We did not have a sufficient sample size to test the sensitivity of the range limit in Peru because the time series of Landsat imagery was much shorter for this region.

In general, there was a positive relationship between standard deviation in mangrove EVI and standard deviation in precipitation and temperature across range limits (Figure 6). However, there were some exceptions to this pattern. For example, the range limit in Brazil exhibited relatively low variability in EVI, but high variability in temperature

and precipitation. At the range limit in Peru, where EVI was also relatively stable, variability in temperature was low, but variability in precipitation was the highest of all range limits in the study.

3.4 | Temporal variability in salt marsh EVI

If variability in EVI of salt marshes near the range limit was especially high, then this pattern could be due to the fact that these range edge bins contained a higher proportion of salt marsh vegetation. However, the standard deviation of EVI for salt marshes near each of these range limits was lower than the standard deviation for mangrove at the corresponding range limit (Supporting Information Figure S5).

4 | DISCUSSION

Macroclimatic variables such as temperature and precipitation are important in controlling the distribution, abundance and diversity of mangroves (Duke et al., 1998; Hutchison, Manica, Swetnam, Balmford,

TABLE 2 Standardized regression coefficients for effects of annual minimum temperature and precipitation in multiple linear regression between changes in mean annual enhanced vegetation index (EVI) and climatic variables

	Range limit	1° equatorward	2° equatorward	3° equatorward	4° equatorward
USA – Atlantic (29.5°)					
Minimum temperature	**.37**	**.47**	.28	−.05	−.37
Precipitation	.12	.09	.09	**.41**	.36
USA – Gulf of Mexico (28.5°)					
Minimum temperature	**.41**	na	.20	na	.24
Precipitation	**.44**	na	.19	na	.39
Brazil (−28°)					
Minimum temperature	−.27	−.09	−.01	.10	−.31
Precipitation	.03	−.08	.06	.26	.05
Mexico – Pacific (27°)					
Minimum temperature	−.31	.08	.19	na	na
Precipitation	.45	.22	.33	na	na
Mexico – Gulf of California (29.5°)					
Minimum temperature	.49	−.18	.12	.09	−.23
Precipitation	−.13	**.39**	**.44**	−.02	.10
Peru (−4°)					
Minimum temperature	na	na	na	na	na
Precipitation	na	na	na	na	na

na = regressions were not calculated because either there were no mangroves in the latitudinal bin or time series was not of sufficient length. *Note.* Bold values are significant at *p* < .1. Latitude of range limit is provided for each region.

& Spalding, 2014; Rovai et al., 2016). In the case of temperature, it appears that extremes (e.g. annual minimum temperature) play a larger

role in setting range limits than means do (Cavanaugh et al., 2015; Osland et al., 2013; this study). However, there is evidence that climate thresholds for presence, abundance and diversity of mangroves are range limit specific (Osland, Feher, et al., 2017). We found that spatial relationships between a measure of performance, EVI, and minimum temperature and precipitation were also range limit specific (Figure 3). Furthermore, temporal trends and variability in EVI and the drivers of that variability differed across range limits (Figure 5, Table 2). Below we discuss in more detail these differences in the strength of (a) linear trends in EVI, (b) interannual variability in EVI, and (c) relationships between variability in EVI and climatic variables. Ultimately, we argue that these results suggest substantial variability in the relative importance of processes that control mangrove range limits around the Americas.

Mangrove range limits in the southeastern USA, the Pacific coast of Mexico, and Brazil exhibited significant positive linear trends in EVI over the study period, although the strength of greening varied across regions. These positive trends are unlikely to be confounded by changes in adjacent salt marsh as salt marshes near the mangrove range limits did not show consistent increases in EVI (Supporting Information Table S1). Previous studies have documented recent increases in mangrove cover at range limits along the Atlantic USA coast in Florida (Cavanaugh et al., 2014; Rodriguez, Feller, & Cavanaugh, 2016), Louisiana (Giri & Long, 2016; Giri, Long, & Tieszen, 2011; Osland, Day, et al., 2017), and the northwestern Gulf of Mexico coast in Texas (Armitage et al., 2015; Sherrod & McMillan, 1985), where we observed especially high rates of increase in EVI. We hypothesize that greening at these mangrove range limits is due to expansion of mangroves into adjacent marsh or unvegetated habitat. Although we did not explicitly map mangrove expansion [mangrove habitat was defined by the static
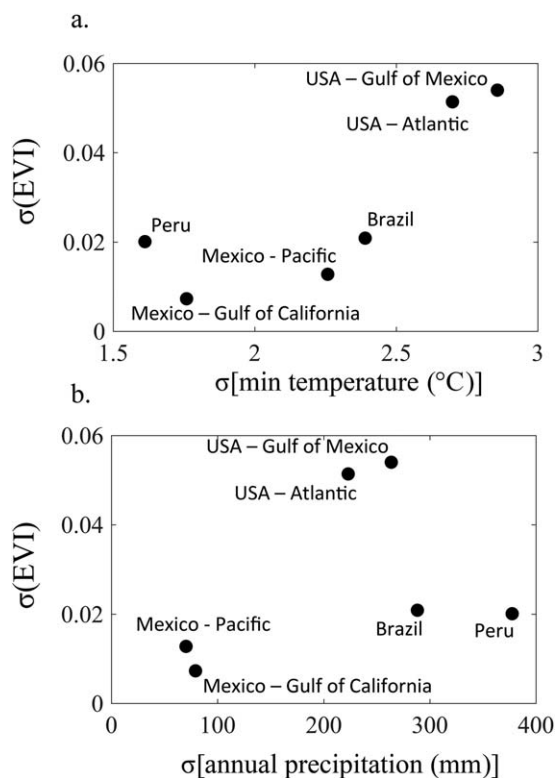
FIGURE 6 Relationship between standard deviation of annual enhanced vegetation index (EVI) and standard deviation of (a) annual minimum temperature, and (b) annual precipitation

Giri et al. (2011) and Spalding et al. (2010) datasets], the resolution of Landsat is 30 m and so a single 900-m^2 pixel will likely contain a mix of mangrove canopy and other land cover types (e.g. bare soil, water, marsh). Increases in the fractional canopy cover (i.e. leaf area index or canopy closure) of a pixel over time would lead to an increase in EVI (Green et al., 1997). These positive trends in EVI at mangrove range limits mirror recent greening that has been observed in another ecotonal region – the southern boundary of tundra ecosystems in North America (Goetz, Bunn, Fiske, & Houghton, 2005; Verbyla, 2008), where enhanced photosynthetic activity has been attributed to recent warming. It is important to note the temporal coverage of our study (1984–2011) as there is evidence that recent expansion in some regions (e.g. near range limits in the southeast USA) is part of a longer-term cycle between mangrove and salt marsh dominance (Giri & Long, 2016; Osland, Day, et al., 2017; Rodriguez et al., 2016). Expansion has not been observed at the poleward mangrove range limits in Brazil, Mexico and Peru (Saintilan et al., 2014; Soares, Estrada, Fernandez, & Tognella, 2012), and here we found weak or insignificant trends in EVI.

At some of our range limit regions, EVI trends were punctuated by major disturbance events. The largest of these was a dramatic decline in EVI in 1990 at both the Atlantic USA and northwestern Gulf of Mexico range limits in eastern North America. It took between 3–6 years for EVI to recover to pre-1990 levels after this disturbance. This decline in EVI corresponds with a severe freeze in late December of 1989 that caused large-scale mangrove mortality across the southeast USA (Montague & Odum, 1997; Zhang et al., 2016). A less pronounced decline in EVI was observed between 1989 and 1991 at the range limit in the Gulf of California region of Mexico. This decline corresponds to a large La Niña event in 1989 that was associated with decreased precipitation in the Gulf of California (Bernal, Ripa, & Herguera, 2001).

While studies that examine variability in abundance across a species' range are relatively rare, there is some support for the hypothesis that variability in abundance increases towards range edges (Sexton et al., 2009). For example, Williams, Ives, and Applegate (2003) found this pattern in three small game species and attributed it to increased environmentally driven density-independent fluctuations in abundance at range edges. We found gradients in EVI variability along the Atlantic and Gulf of Mexico coasts of North America, with variability highest at the range limit (Figure 5). These patterns indicate that the Atlantic USA and northwestern Gulf of Mexico range limits are close to the limits of their climatic tolerances. High temporal variability in key climatic variables drives relatively frequent increases and decreases in abundance and productivity in these regions (Osland, Day, et al., 2017; Rodriguez et al., 2016; Sherrod & McMillan, 1985). The lower standard deviation for salt marshes compared to mangroves in these regions indicates that it is unlikely that the positive latitudinal trends found in mangrove EVI over the study period are confounded by changes in adjacent salt marshes. Contrary to expectation, variability in EVI did not increase towards range limits for the sites in South America or the Pacific coast of North America. In these regions, the annual variability of EVI at range limits tended to be stable through time.

The regression analyses presented in Table 2 provide further support for the idea that range limits in eastern North America are sensitive to climate variables. We found significant relationships between annual changes in EVI and annual minimum temperature at the Atlantic USA range limit in Florida. Changes in EVI were correlated with both annual minimum temperature and annual precipitation at the northwestern Gulf of Mexico range limit in Texas. These results agree with a correlative distribution model-based study that argued that the distribution limits, abundance, and species richness of mangroves are controlled by temperature in eastern North America and both temperature and precipitation in the western Gulf of Mexico (Osland, Feher, et al., 2017). The surprising negative relationship between EVI changes and minimum temperature for the 25.5° latitudinal bin on the Atlantic coast of USA may be due to a confounding environmental factor. A large decline in EVI in this area was observed in 1992, which was the same year that Hurricane Andrew made landfall in south Florida. Other studies have documented the negative impacts of this storm on mangrove populations in south Florida (Zhang et al., 2016). The winter of 1991–1992 experienced above average minimum temperatures in this area, which may have biased the regression analysis. Changes in EVI were positively associated with precipitation on the west coast of North America, but there were no latitudinal patterns in the strength of this relationship. The lack of latitudinal pattern may be due to the relatively small range in precipitation found across the latitudinal gradient analysed in these regions (Supporting Information Figure S3). We did not find significant relationships between EVI changes and either minimum temperature or precipitation at the range limit on the east coast of South America in Brazil (Table 2).

Range limits with low EVI variability (e.g. Mexico, Brazil and Peru) may be controlled by non-climatic processes such as dispersal limitation (scenario B in Figure 1) or temporal variability in key climate drivers may be low in these regions (scenario C in Figure 1). In scenario C, climatic extremes may not be the primary control on range limitation. Instead, demographic rates such as growth and birth may be controlled by long-term mean climate, which could make it difficult to identify temporal relationships between population dynamics and climate variability. The Gulf of California coast of Mexico exhibited low variability in both minimum temperature and precipitation (Figure 6). As annual changes in EVI in this region were also somewhat sensitive to precipitation (Table 2) and spatial patterns in EVI matched patterns in precipitation and minimum temperature (Figure 3), we suggest that this range limit is an example of scenario C. The mangrove range limit in southern Australia provides another example of this scenario. Here, mean winter temperatures are low, but extreme cold events are rare (Osland, Feher, et al., 2017) and mangrove adaptations to these conditions lead to slow growth and low reproductive success (Stuart, Choat, Martin, Holbrook, & Ball, 2007).

The range limits on the Pacific coast of Mexico, Brazil, and Peru exhibited higher variability in at least one of the climate factors thought to control range limitation in those regions (Figure 6). Brazil and the Pacific coast of Mexico experienced moderate variability in minimum temperature and Peru experienced high variability in precipitation. The high climate variability coupled with low variability in mangrove EVI may indicate that these range limits are at least partially controlled by dispersal limitation and/or lack of available habitat for expansion (scenario B in Figure 1; Saintilan et al., 2014; Soares et al., 2012; Ximenes, Maeda, Arcoverde, & Dahdouh-Guebas, 2016). Some transplant experiments provide additional support for the role of dispersal limitation on the west

coasts of North and South America. In the 1950s, a species of mangrove native to the Indo-West Pacific, *Avicennia marina*, was introduced to Mission Bay, San Diego, which is more than 600 km north of the current range limit of mangroves on the west coast of North America (Moseman, Zhang, Qian, & Levin, 2009). This population has persisted for more than 50 years in the face of multiple eradication efforts. While *A. marina* is a different species than the *Avicennia germinans* native to the Americas, morphological and physiological traits are similar for congeneric mangrove species (Ellison, Farnsworth, & Merkt, 1999), which may indicate suitable habitat for *A. germinans* north of its current range limit. Similarly, mangroves that were planted in the mid-1980s in Peru near the southern range limit on the Pacific coast of South America have persisted and expanded over the past 30 years (Saintilan et al., 2014). Equatorward flowing western boundary currents along the Pacific coasts of North and South America may act to limit poleward dispersal of mangroves in these regions. Local equatorward currents have been identified as a potential range limiting factor on the east coast of South America (Soares et al., 2012). This is not to say that temperature and precipitation are unimportant in these regions. Mangrove species richness near each of these range limit regions is strongly correlated with temperature or precipitation (Osland, Day, et al., 2017), and global mangrove biomass is correlated with both of these climatic factors (Hutchison et al., 2014; Rovai et al., 2016). Rather, it is possible that there is an interaction between climate and dispersal limitation at these range limits. Climatic conditions could lead to lowered growth and reproduction rates, which, when combined with unfavourable ocean current patterns or limited habitat availability, would limit dispersal to suitable sites.

We suggest that our approach of assessing temporal variability in the productivity of range limit populations be used in conjunction with, not in place of, spatial distribution models. Unlike environmental niche models that compare species' distributions to climatic data, this approach of examining temporal variability in vegetation productivity does not assume that species' distributions are in equilibrium with their environment. As a result, it can be useful for identifying situations where range limits are controlled by dispersal or biotic interactions instead of climate or where range limits are in the process of expanding or contracting. However, this is still a correlative analysis, and so caution is warranted when making inferences into the causal drivers of range limitation. For example, this study was limited to two of the putative drivers of poleward mangrove range limits: air temperature and precipitation. Sea surface temperature has often been used to characterize global mangrove distributions (Duke et al., 1998), but air temperature and precipitation are expected to have a more direct impact on mangrove distribution and productivity (Osland, Feher, et al., 2017).

Ideally this method would be applied to direct measurements of population dynamics. Here we have used EVI as a proxy for mangrove abundance as EVI is highly correlated with mangrove cover in our study area. Increases in population sizes near range limits will lead to increases in canopy cover and increases in greenness, while mortality events (i.e. severe freezes) can be identified from reductions in vegetation indices such as EVI (Zhang et al., 2016). However, we recognize that vegetation indices can also reflect processes such as tree growth that are not necessarily related to population changes. Remotely sensed proxies for abundance or performance provide a practical way to estimate dynamics over large areas; however, we echo Gaston's (2009) call for studies that more directly measure population size and demographic rates along species' distributions.

Another limitation of this study is our inability to identify the distributions of different species, phenotypes and genotypes of mangroves. Mangrove species vary in their ability to tolerate cold temperatures (Cavanaugh et al., 2015; Cook-Patton, Lehmann, & Parker, 2015; Devaney, Lehmann, Feller, & Parker, 2017; Stuart et al., 2007), salinity and other environmental factors (Lovelock, Krauss, Osland, Reef, & Ball, 2016; Lugo & Snedaker, 1974). Thus, species may respond differently to variability in temperature and precipitation, confounding relationships between EVI and climatic factors. However, this effect is likely to be limited near poleward range limits where species diversity is low. The three to four species located in our study area have similar distributions and therefore similar realized niches (Spalding et al., 2010). Nevertheless, additional work is needed to characterize species-level variability in the relationships between productivity and climate variables. In addition, genetic variation at range edges has the potential to enable adaptation at range limits under certain conditions (Sexton et al., 2009). Local adaptation could reduce the sensitivity of edge populations to climate fluctuations and dampen variability in population dynamics. As a result, populations along a species' distribution may respond differently to environmental conditions. Significant genetic structure has been observed among mangrove populations near range limits in the Gulf of California (Sandoval-Castro et al., 2012, 2014); however, these populations have low genetic diversity and it is unclear whether local adaptation is occurring in these populations.

In summary, our results demonstrate how the processes that control range limitation can vary among range limits of the same species or related group of species. EVI of mangroves near their poleward range limits in eastern North America was highly variable and this variability was closely associated with climatic factors. There has been a strong linear greening trend in these regions, which we interpret as expansion of mangroves due to decreases in the frequency of extreme cold events. The sensitivity of mangroves in eastern North America to climatic variability suggests that range limits in this region are strongly controlled by climate. In contrast, EVI of mangrove range limits in western North America, eastern South America and western South America is less variable and not as sensitive to short-term climatic fluctuations. Other processes such as dispersal limitation or lack of habitat may be interacting with climatic factors to control these range limits. Variability in the factors that control range limits across regions has important implications for the impacts of future climate change on mangrove range limits. Mangrove expansion or contraction in response to climate change may be rapid in regions that are highly sensitive to climate variability. However, the response of range limits is likely to be more complex in regions where additional processes influence the abundance and distribution of mangroves.

ACKNOWLEDGMENTS

DATA ACCESSIBILITY

All datasets used in this study are publicly available. See references (Giri, Ochieng, et al., 2011; Google Earth Engine Team, 2015; Sheffield et al., 2006; Spalding et al., 2010) for more details.

ORCID

Kyle C. Cavanaugh http://orcid.org/0000-0002-3313-0878

REFERENCES

Armitage, A. R., Highfield, W. E., Brody, S. D., & Louchouarn, P. (2015). The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. *PLoS One*, 10, e0125404–e0125417.

Bernal, G., Ripa, P., & Herguera, J. C. (2001). Oceanographic and climatic variability in the lower gulf of California : Links with the tropics and north Pacific. *Ciencias Marinas*, 27, 595–617.

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences USA*, 111, 723–727.

Cavanaugh, K. C., Parker, J. D., Cook-Patton, S. C., Feller, I. C., Williams, A. P., & Kellner, J. R. (2015). Integrating physiological threshold experiments with climate modeling to project mangrove species' range expansion. *Global Change Biology*, 21, 1928–1938.

Cook-Patton, S. C., Lehmann, M., & Parker, J. D. (2015). Convergence of three mangrove species towards freeze-tolerant phenotypes at an expanding range edge. *Functional Ecology*, 29, 1332–1340.

Devaney, J. L., Lehmann, M., Feller, I. C., & Parker, J. D. (2017). Mangrove microclimates alter seedling dynamics at the range edge. *Ecology*, 98, 2513–2520.

Duke, N. C., Ball, M. C., & Ellison, J. C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, 7, 27–47.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.

Ellison, A. M., Farnsworth, E. J., & Merkt, R. E. (1999). Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*, 8, 95–115.

Ewel, K. C., Twilley, R. R., & Ong, J. E. (1998). Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters*, 7, 83–94.

Feher, L. C., Osland, M. J., Griffith, K. T., Grace, J. B., Howard, R. J., Stagg, C. L., ... Rogers, K. (2017). Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands. *Ecosphere*, 8, e01956.

Feng, M., Sexton, J. O., Huang, C., Masek, J. G., Vermote, E. F., Gao, F., ... Townshend, J. R. (2013). Global surface reflectance products from Landsat: Assessment using coincident MODIS observations. *Remote Sensing of Environment*, 134, 276–293.

Gabler, C. A., Osland, M. J., Grace, J. B., Stagg, C. L., Day, R. H., Hartley, S. B., ... McLeod, J. L. (2017). Macroclimatic change expected to transform coastal wetland ecosystems this century. *Nature Climate Change*, 7, 142–147.

Gaston, K. J. (2009). Geographic range limits: Achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1395–1406.

Giri, C., & Long, J. (2016). Is the geographic range of mangrove forests in the conterminous United States really expanding? *Sensors*, 16, 2010.

Giri, C., Long, J., & Tieszen, L. (2011). Mapping and monitoring Louisiana's mangroves in the aftermath of the 2010 Gulf of Mexico oil spill. *Journal of Coastal Research*, 277, 1059–1064.

Giri, C., Ochieng, E., Tieszen, L. L., Zhu, Z., Singh, A., Loveland, T., ... Duke, N. (2011). Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, 20, 154–159. Retrieved from https://databasin.org/datasets/d214245ab4554bc1a1e7e7d9b45b9329

Giri, C., Pengra, B., Zhu, Z., Singh, A., & Tieszen, L. L. (2007). Monitoring mangrove forest dynamics of the Sundarbans in Bangladesh and India using multi-temporal satellite data from 1973 to 2000. *Estuarine, Coastal and Shelf Science*, 73, 91–100.

Goetz, S. J., Bunn, A. G., Fiske, G. J., & Houghton, R. A. (2005). Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences USA*, 102, 13521–13525.

Google Earth Engine Team. (2015). *Google earth engine: A planetary-scale geospatial analysis platform*. Retrieved from https://earthengine.google.com

Green, E. P., Mumby, P. J., Edwards, A. J., Clark, C. D., & Ellis, A. C. (1997). Estimating leaf area index of mangroves from satellite data. *Aquatic Botany*, 58, 11–19.

Hutchison, J., Manica, A., Swetnam, R., Balmford, A., & Spalding, M. (2014). Predicting global patterns in mangrove forest biomass. *Conservation Letters*, 7, 233–240.

Jiang, Z., Huete, A. R., Didan, K., & Miura, T. (2008). Development of a two-band enhanced vegetation index without a blue band. *Remote Sensing of Environment*, 112, 3833–3845.

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12, 334–350.

Kovacs, J. M., Wang, J., & Flores-Verdugo, F. (2005). Mapping mangrove leaf area index at the species level using IKONOS and LAI-2000 sensors for the Agua Brava Lagoon, Mexican Pacific. *Estuarine, Coastal and Shelf Science*, 62, 377–384.

López-Medellín, X., Ezcurra, E., González-Abraham, C., Hak, J., Santiago, L. S., & Sickman, J. O. (2011). Oceanographic anomalies and sea-level rise drive mangroves inland in the Pacific coast of Mexico. *Journal of Vegetation Science*, 22, 143–151.

Lovelock, C. E., Krauss, K. W., Osland, M. J., Reef, R., & Ball, M. C. (2016). The physiology of mangrove trees with changing climate. In G. Goldstein and L. S. Santiago (Eds.), *Tropical tree physiology: Adaptations and responses in a changing environment* (pp. 149–179). New York: Springer.

Lugo, A. E., & Snedaker, S. C. (1974). The ecology of mangroves. *Annual Review of Ecology and Systematics*, 5, 39–64.

Montague, C. L., & Odum, H. T. (1997). The intertidal marshes of Florida's Gulf Coast. In C. L. Coultas & Y. P. Hsieh (Eds.), *Ecology and management of tidal marshes: A model from the Gulf of Mexico* (pp. 1–33). Delray Beach, FL: St. Lucie Press.

Moseman, S. M., Zhang, R., Qian, P. Y., & Levin, L. A. (2009). Diversity and functional responses of nitrogen-fixing microbes to three wetland invasions. *Biological Invasions*, 11, 225–239.

Osland, M. J., Day, R. H., Hall, C. T., Brumfield, M. D., Dugas, J. L., & Jones, W. R. (2017). Mangrove expansion and contraction at a poleward range limit: Climate extremes and land-ocean temperature gradients. *Ecology, 98*, 125–137.

Osland, M. J., Enwright, N., Day, R. H., & Doyle, T. W. (2013). Winter climate change and coastal wetland foundation species: Salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology, 19*, 1482–1494.

Osland, M. J., Enwright, N. M., Day, R. H., Gabler, C. A., Stagg, C. L., & Grace, J. B. (2016). Beyond just sea-level rise: Considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology, 22*, 1–11. https://doi.org/10.1111/gcb.13084.

Osland, M. J., Enwright, N. M., & Stagg, C. L. (2014). Freshwater availability and coastal wetland foundation species: Ecological transitions along a rainfall gradient. *Ecology, 95*, 2789–2802.

Osland, M. J., Feher, L. C., Griffith, K. T., Cavanaugh, K. C., Enwright, N. M., Day, R. H., . . . Rogers, K. (2017). Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs, 87*, 341–359.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature, 421*, 37–42.

Quisthoudt, K., Schmitz, N., Randin, C. F., Dahdouh-Guebas, F., Robert, E. M. R., & Koedam, N. (2012). Temperature variation among mangrove latitudinal range limits worldwide. *Trees - Structure and Function, 26*, 1919–1931.

Record, S., Charney, N. D., Zakaria, R. M., & Ellison, A. M. (2013). Projecting global mangrove species and community distributions under climate change. *Ecosphere, 4*, art34–art23.

Rodriguez, W., Feller, I. C., & Cavanaugh, K. C. (2016). Spatio-temporal changes of a mangrove-saltmarsh ecotone in the northeastern coast of Florida, USA. *Global Ecology and Conservation, 7*, 245–261.

Rovai, A. S., Riul, P., Twilley, R. R., Castañeda-Moya, E., Rivera-Monroy, V. H., Williams, A. A., . . . Pagliosa, P. R. (2016). Scaling mangrove aboveground biomass from site-level to continental-scale. *Global Ecology and Biogeography, 25*, 286–298.

Saenger, P. (2002). *Mangrove ecology, silviculture and conservation.* Dordrecht, Netherlands: Kluwer Academic Publishers.

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology, 20*, 147–157.

Sandoval-Castro, E., Dodd, R. S., Riosmena-Rodríguez, R., Enriquez-Paredes, L. M., Tovilla-Hernández, C., Lo ez-Vivas, J. M., . . . Muñiz-Salazar, R. (2014). Post-glacial expansion and population genetic divergence of mangrove species *Avicennia germinans* (L.) Stearn and *Rhizophora mangle* L. along the Mexican coast. *PLoS One, 9*, e93358.

Sandoval-Castro, E., Muñiz-Salazar, R., Enríquez-Paredes, L. M., Riosmena-Rodríguez, R., Dodd, R. S., Tovilla-Hernández, C., & Arredondo-García, M. C. (2012). Genetic population structure of red mangrove (*Rhizophora mangle* L.) along the northwestern coast of Mexico. *Aquatic Botany, 99*, 20–26.

Schaeffer-Novelli, Y., Cintrón-Molero, G., Adaime, R. R., de Camargo, T. M., Cintron-Molero, G., & de Camargo, T. M. (1990). Variability of mangrove ecosystems along the Brazilian coast. *Estuaries, 13*, 204–218.

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics, 4*, 415–436.

Sherrod, C. L., & McMillan, C. (1981). Black mangrove, Avicennia germinans, in Texas: Past and present distribution. *Contributions in Marine Science, 24*, 115–131.

Sherrod, C. L., & McMillan, C. (1985). The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science, 28*, 129–140.

Soares, M. L. G., Estrada, G. C. D., Fernandez, V., & Tognella, M. M. P. (2012). Southern limit of the Western South Atlantic mangroves: Assessment of the potential effects of global warming from a biogeographical perspective. *Estuarine, Coastal and Shelf Science, 101*, 44–53.

Spalding, M., Kainuma, M., & Collins, L. (2010). *World atlas of mangroves*. New York: Earthscan. Retrieved from http://data.unep-wcmc.org/datasets/5

Stuart, S. A., Choat, B., Martin, K. C., Holbrook, N. M., & Ball, M. C. (2007). The role of freezing in setting the latitudinal limits of mangrove forests. *The New Phytologist, 173*, 576–583.

Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology, 12*, 686–702.

Verbyla, D. (2008). The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecology and Biogeography, 17*, 547–555.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., . . . Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences, 281*, 20140846–20140810.

Webb, W. L., Lauenroth, W. K., Szarek, S. R., & Kinerson, R. S. (1983). Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. *Ecology, 64*, 134–151.

Williams, C. K., Ives, A. R., & Applegate, R. D. (2003). Population dynamics across geographical ranges : Time-series analyses of three small game species. *Ecology, 84*, 2654–2667.

Ximenes, A. C., Maeda, E. E., Arcoverde, G. F. B., & Dahdouh-Guebas, F. (2016). Spatial assessment of the bioclimatic and environmental factors driving mangrove tree species' distribution along the Brazilian coastline. *Remote Sensing, 8*, 451.

Zhang, K., Thapa, B., Ross, M., & Gann, D. (2016). Remote sensing of seasonal changes and disturbances in mangrove forest : A case study from South Florida. *Ecosphere, 7*, e01366–e01323.

BIOSKETCH

KYLE CAVANAUGH is a geographer and ecologist interested in the processes that control the range limits of coastal foundation species.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Table S1. Linear trends in mean annual EVI (1984-2011) for saltmarsh sites near mangrove range limits. Slopes represent changes in EVI (unitless) per year

Region	R^2	slope	*P*-value
USA - Atlantic	0.05	-2.6E-04	0.26
USA – Gulf of Mexico	0.53	0.004	< 0.01
Brazil	0.07	7.4E-04	0.18
Mexico - Pacific	0.20	6.5E-04	0.03
Mexico - Gulf of California	0.17	-2.2E-04	0.03
Peru	0.16	-4.9E-04	0.14
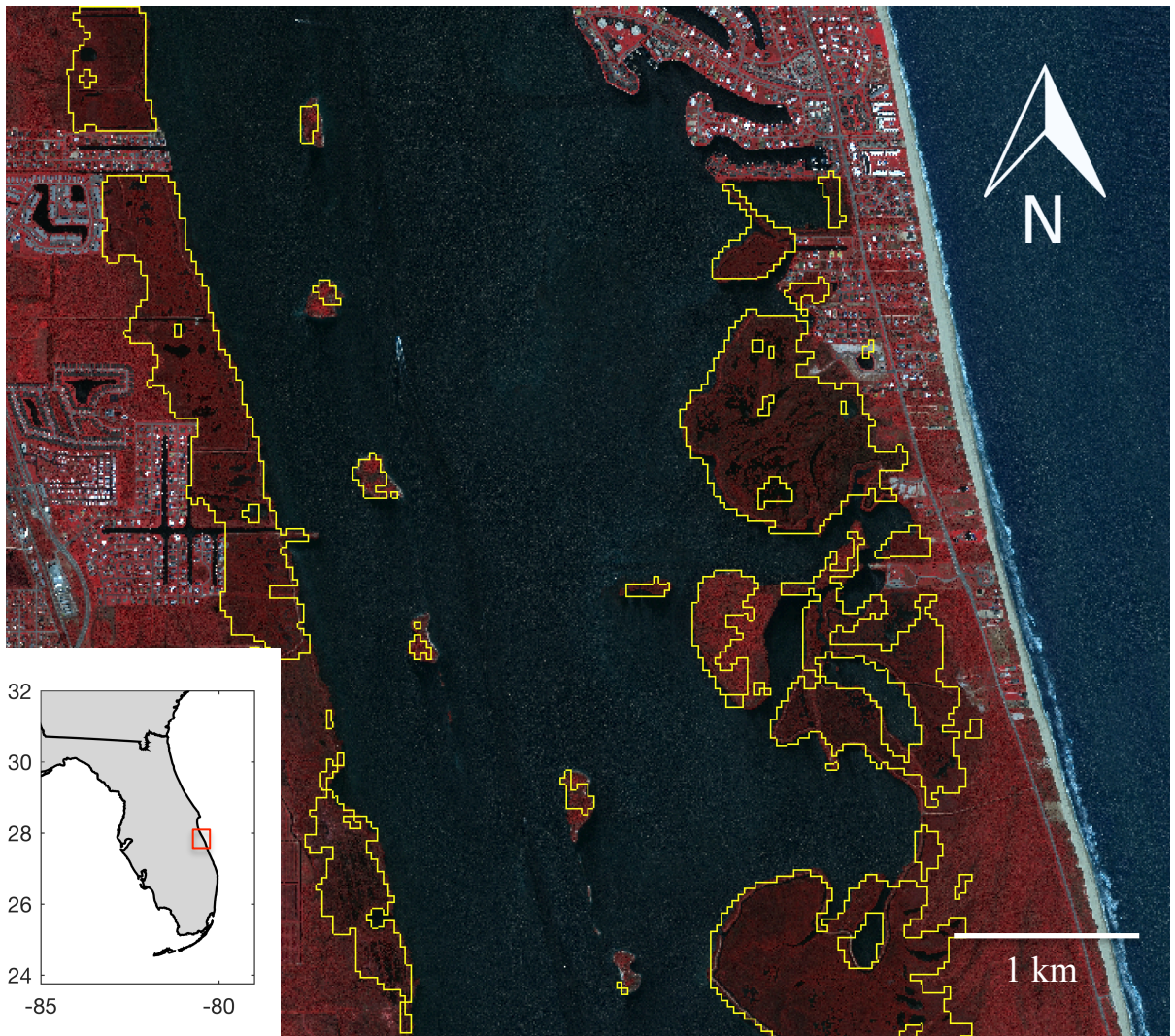
Figure S1. IKONOS image used to compare Landsat EVI to percent mangrove cover. The mangrove areas identified by the Giri et al. (2011) dataset are outlined in yellow.

$R^2 = 0.69$
$p < 0.01$

mean EVI (Landsat)
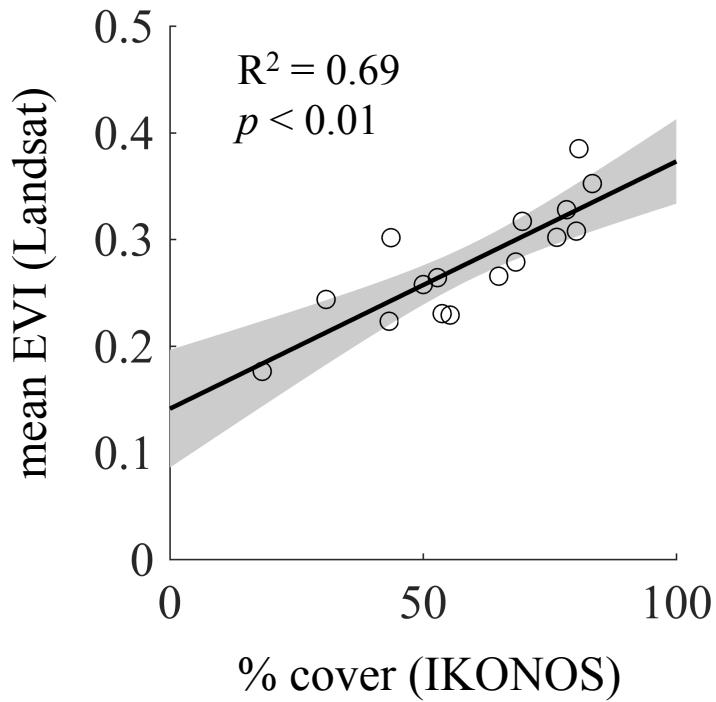
% cover (IKONOS)

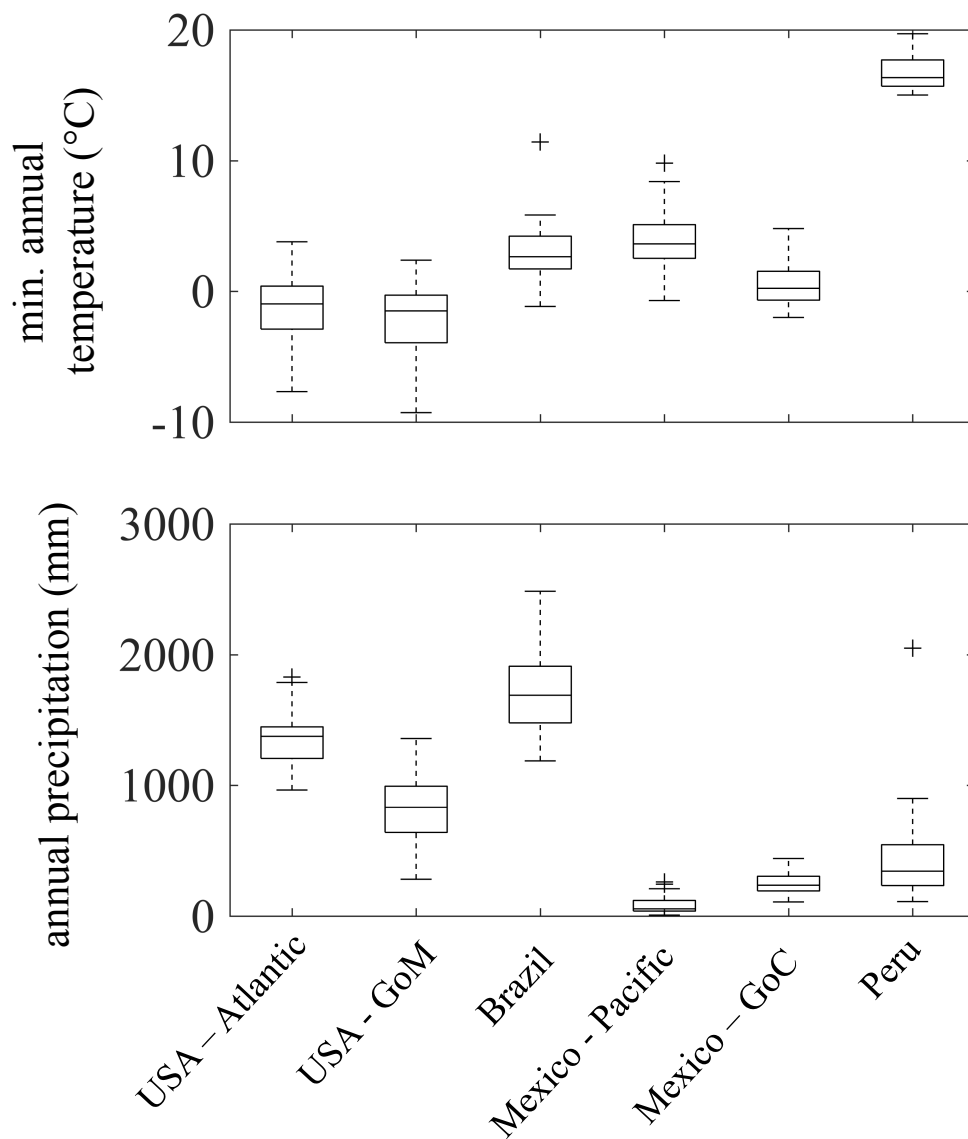Figure S2. Relationship between Landsat EVI and percent cover as measured from 1-m resolution IKONOS imagery.

Figure S3. Box plots of data for minimum annual temperature and annual precipitation from 1984-2011 for range edges. On each box, the center line represents the median, the top and bottom edges represent the 25th and 75th percentiles, the whiskers extend to the most extreme points not considered outliers and the plus symbols represent outliers.
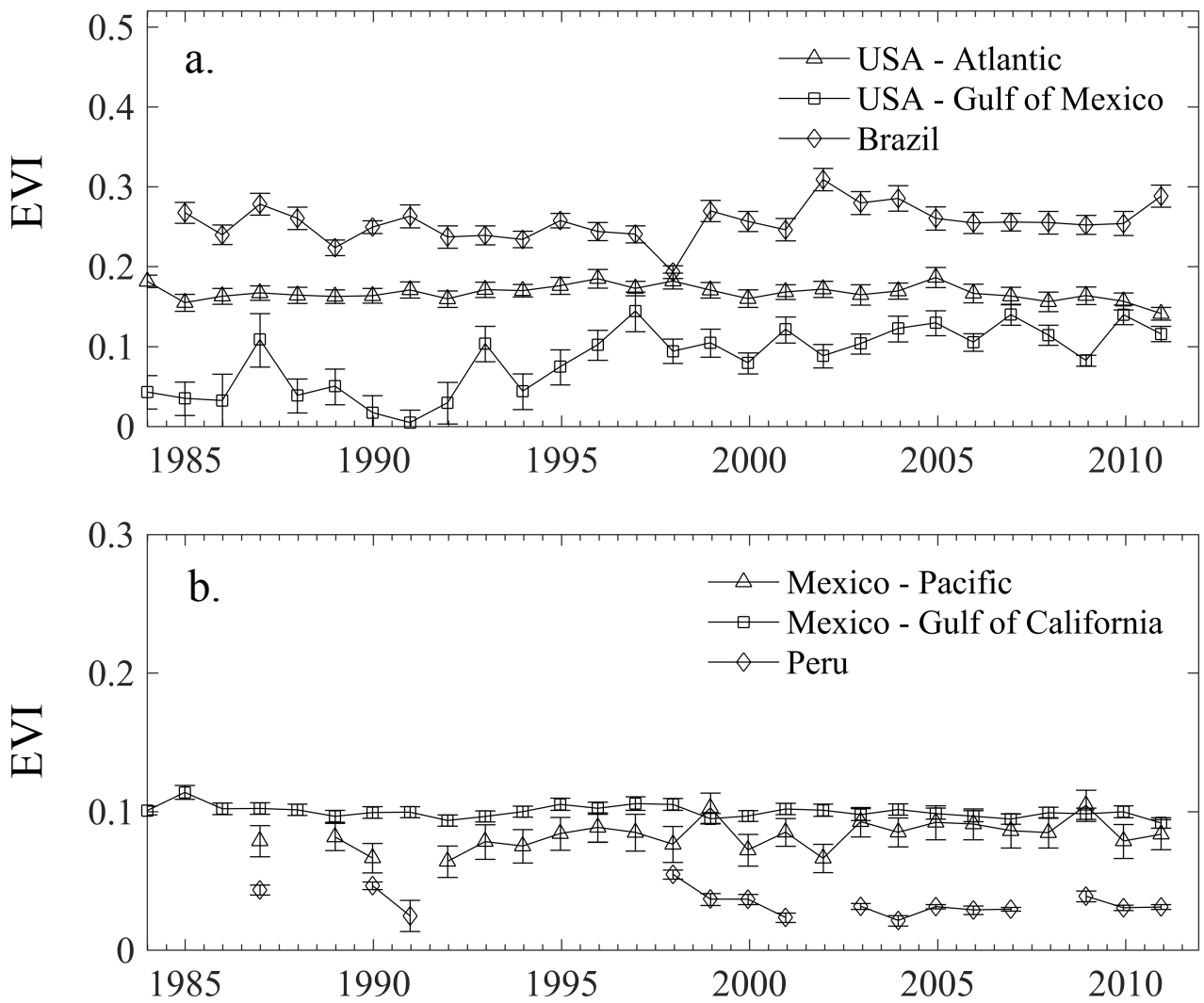
Figure S4. Time series of mean annual EVI for salt marsh sites near mangrove range limits on (a) Atlantic and (b) Pacific coasts of North America. Error bars represent 95% percent confidence intervals.
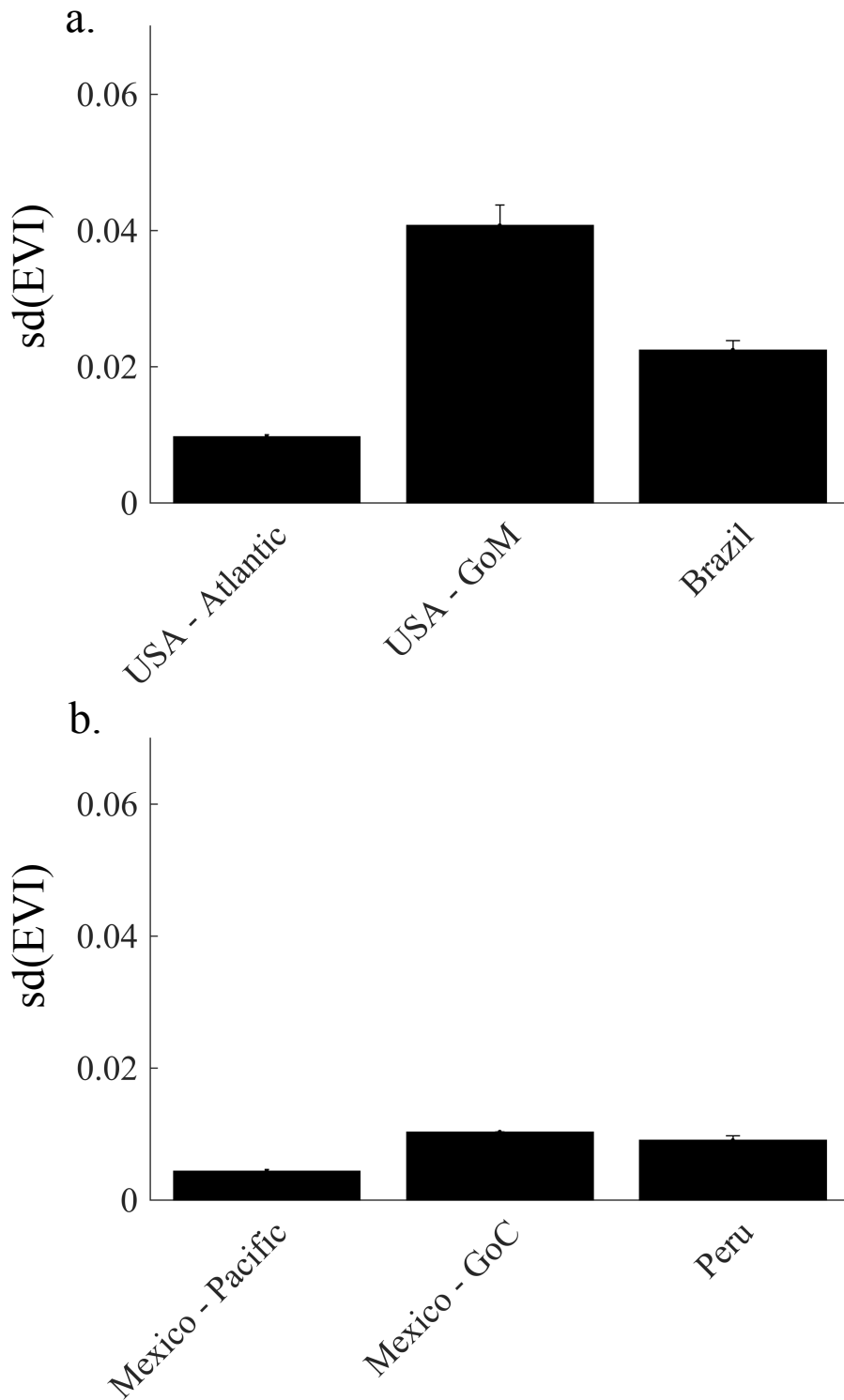
Figure S5. Standard deviation (sd) of mean annual EVI for salt marshes near mangrove range limits on Atlantic (a) and Pacific (b) coasts of North America. Error bars represent 95% percent confidence intervals.
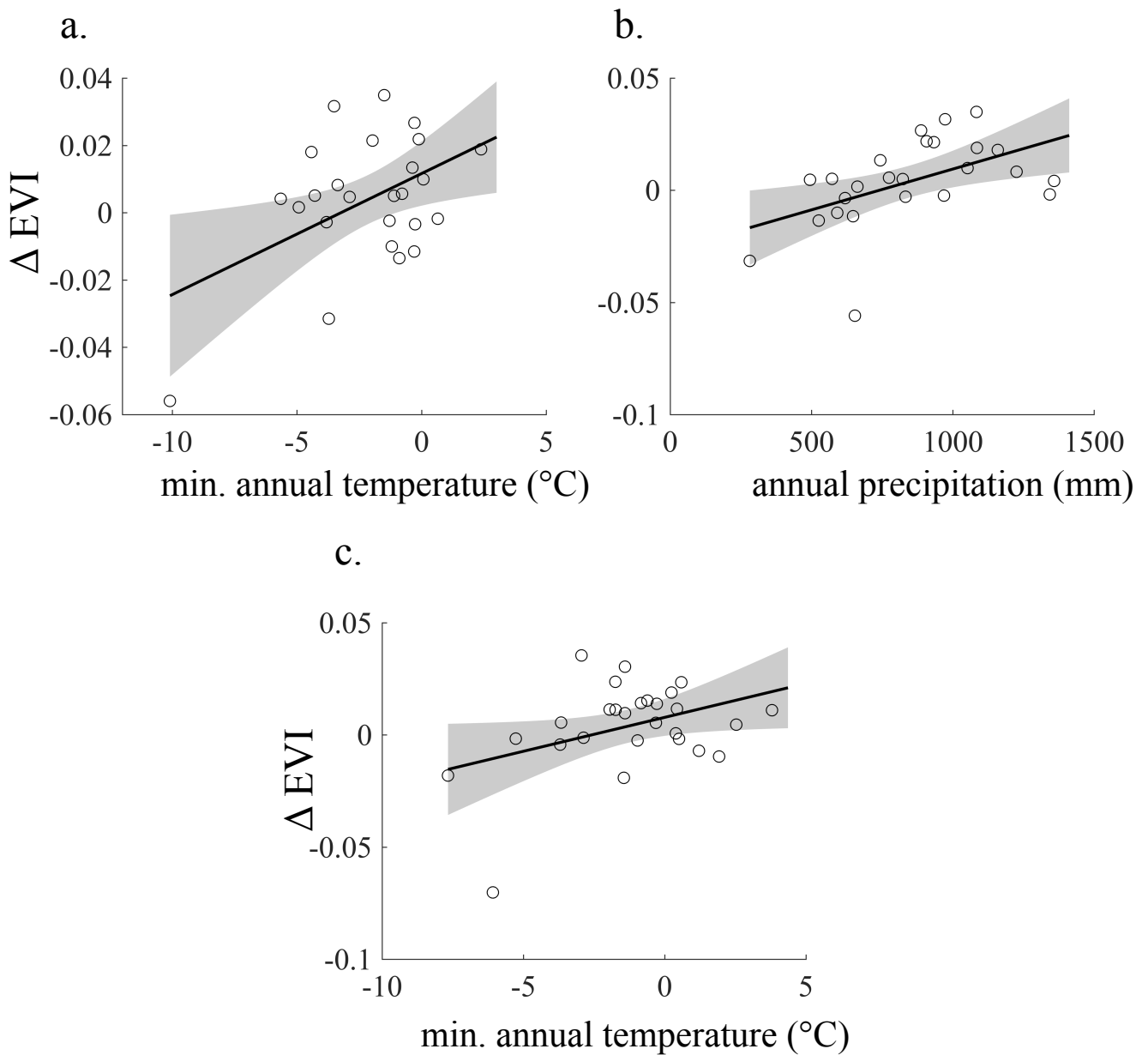
Figure S6. (a) Relationship between annual change in EVI and minimum annual temperature for USA – Gulf of Mexico. (b) Relationship between annual change in EVI and annual precipitation for USA – Gulf of Mexico. (c) Relationship between annual change in EVI and minimum annual temperature for USA – Atlantic.