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SPECIAL FEATURE: EXTREME COLD SPELLS

Mangrove species' responses to winter air temperature extremes in China

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Abstract. The global distribution and diversity of mangrove forests is greatly influenced by the frequency and intensity of winter air temperature extremes. However, our understanding of how different mangrove species respond to winter temperature extremes has been lacking because extreme freezing and chilling events are, by definition, relatively uncommon and also difficult to replicate experimentally. In this study, we investigated species-specific variation in mangrove responses to winter temperature extremes in China. In 10 sites that span a latitudinal gradient, we quantified species-specific damage and recovery following a chilling event, for mangrove species within and outside of their natural range (i.e., native and non-native species, respectively). To characterize plant stress, we measured tree defoliation and chlorophyll fluorescence approximately one month following the chilling event. To quantify recovery, we measured chlorophyll fluorescence approximately nine months after the chilling event. Our results show high variation in the geographic- and species-specific responses of mangroves to winter temperature extremes. While many species were sensitive to the chilling temperatures (e.g., *Bruguiera sexangula* and species in the *Sonneratia* and *Rhizophora* genera), the temperatures during this event were not cold enough to affect certain species (e.g., *Kandelia obovata*, *Aegiceras corniculatum*, *Avicennia marina,* and *Bruguiera gymnorrhiza*). As expected, non-native species were less tolerant of winter temperature extremes than native species. Interestingly, tidal inundation modulated the effects of chilling. In comparison with other temperature-controlled mangrove range limits across the world, the mangrove range limit in China is unique due to the combination of the following three factors: (1) Mangrove species diversity is comparatively high; (2) winter air temperature extremes, rather than means, are particularly intense and play an important ecological role; and (3) due to afforestation and restoration efforts, several species of non-native mangroves have been introduced beyond their natural range limits. Hence, from a global perspective, mangroves in China provide valuable opportunities to advance understanding of the effects of freezing and chilling temperatures on mangroves. Within the context of climate change, our findings provide a foundation for better understanding and preparing for mangrove species-specific responses to future changes in the duration and intensity of winter temperature extremes.

Key words: chilling temperature; China; climate change; climate extreme; coastal wetland; defoliation; *Kandelia;* leaf *Fv/Fm* value; mangrove; non-native species; *Sonneratia;* Special Feature: Extreme Cold Spells; winter temperature extreme.

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Introduction

Within the context of climate change, ecologists and natural resource managers are increasingly challenged to better understand and prepare for the ecological implications of changes in the duration and intensity of climate extremes (Jentsch et al. 2007, Glick et al. 2011, Smith 2011, Hoover et al. 2014). Near the transition between tropical and temperate climates, the frequency and intensity of winter air temperature extremes (i.e., freezing and chilling air temperatures) are particularly important because they greatly influence species' distributions and the structure and functioning of ecosystems (Woodward 1987, Boucek et al. 2016, Osland et al. 2017*a*). Tropical and subtropical species' tolerances and responses to chilling and freezing temperature extremes are highly variable (Sakai and Larcher 1987, Kozlowski and Pallardy 1997, Larcher 2003). Whereas chilling-sensitive plants are damaged at temperatures above freezing (i.e., chilling temperatures), freezing-sensitive plants are damaged by temperatures below the freezing point (i.e., freezing temperatures; Larcher 2003). Freezing and/or chilling temperature extremes can lead to physiological damage, mortality, and/or range contraction. In contrast, the absence of freezing or chilling temperature extremes can lead to enhanced performance and, in certain cases, the range expansion of tropical and subtropical species (Osland et al. 2013, Cavanaugh et al. 2014, Vergés et al. 2014, Gabler et al. 2017). To better anticipate and prepare for the ecological effects of climate change within and near the tropical–temperate climatic transition zone, there is a need to better understand species-specific responses to winter air temperature extremes. In this study, we examine mangrove species' responses to winter air temperature extremes in China.

Mangrove forests are tidal saline wetland ecosystems that are found along tropical and subtropical coasts. All mangrove species are sensitive to some degree of freezing and/or chilling stress; hence, low air temperature extremes limit the latitudinal distribution of mangroves across the globe (Woodroffe and Grindrod 1991, Saenger 2002, Quisthoudt et al. 2012, Osland et al. 2013, 2017*b*, Cavanaugh et al. 2014, Lovelock et al. 2016, Gabler et al. 2017). During the past four decades, our general understanding of the physiological effects of chilling and freezing temperatures on mangroves has greatly improved (Yang and Lin 1998, Stuart et al. 2007, Krauss et al. 2008, Lovelock et al. 2016). However, our understanding of species-specific mangrove responses to low temperatures has been lacking because extreme freezing and chilling events are, by definition, relatively uncommon and difficult to fully replicate via manipulative experiments (Pickens and Hester 2011, Cook-Patton et al. 2015, Coldren and Proffitt 2017). Hence, there is a need for studies that use in situ measurements immediately following freezing and/or chilling events to improve our understanding of species-specific responses of mangroves to low temperature extremes (e.g., Lugo and Patterson-Zucca 1977, Lonard and Judd 1991, Ross et al. 2009, Osland et al. 2015).

In this study, we examined species-specific variability in mangrove responses to chilling air temperature extremes that occurred in China in 2008 (Fig. 1). Because there is a strong relationship between mangrove species richness and winter temperature extremes (Osland et al. 2017*b*), we hypothesized that there would be a high level of species-specific variability in mangrove tolerance of chilling air temperature extremes. Moreover, since non-native species are often less tolerant of extreme conditions that are not common within their natural range (Sakai and Larcher 1987, Alpert et al. 2000, Hellmann et al. 2008), we expected that species introduced outside of their native range (i.e., non-native species) would be more sensitive to chilling temperature extremes than native species. We tested these hypotheses via a multi-site investigation of mangrove response to a chilling event that occurred in 2008. In 10 sites that span a latitudinal gradient (Fig. 1), we quantified species-specific damage and recovery following the chilling event, for mangrove species within and outside of their natural range (i.e., native and non-native species, respectively). To characterize plant stress, we measured tree defoliation and chlorophyll fluorescence approximately one month following the chilling event. To quantify recovery, we measured chlorophyll fluorescence approximately nine months after the chilling event.

In comparison with other temperature-controlled mangrove range limits, the Chinese mangrove range limit is unique due to the

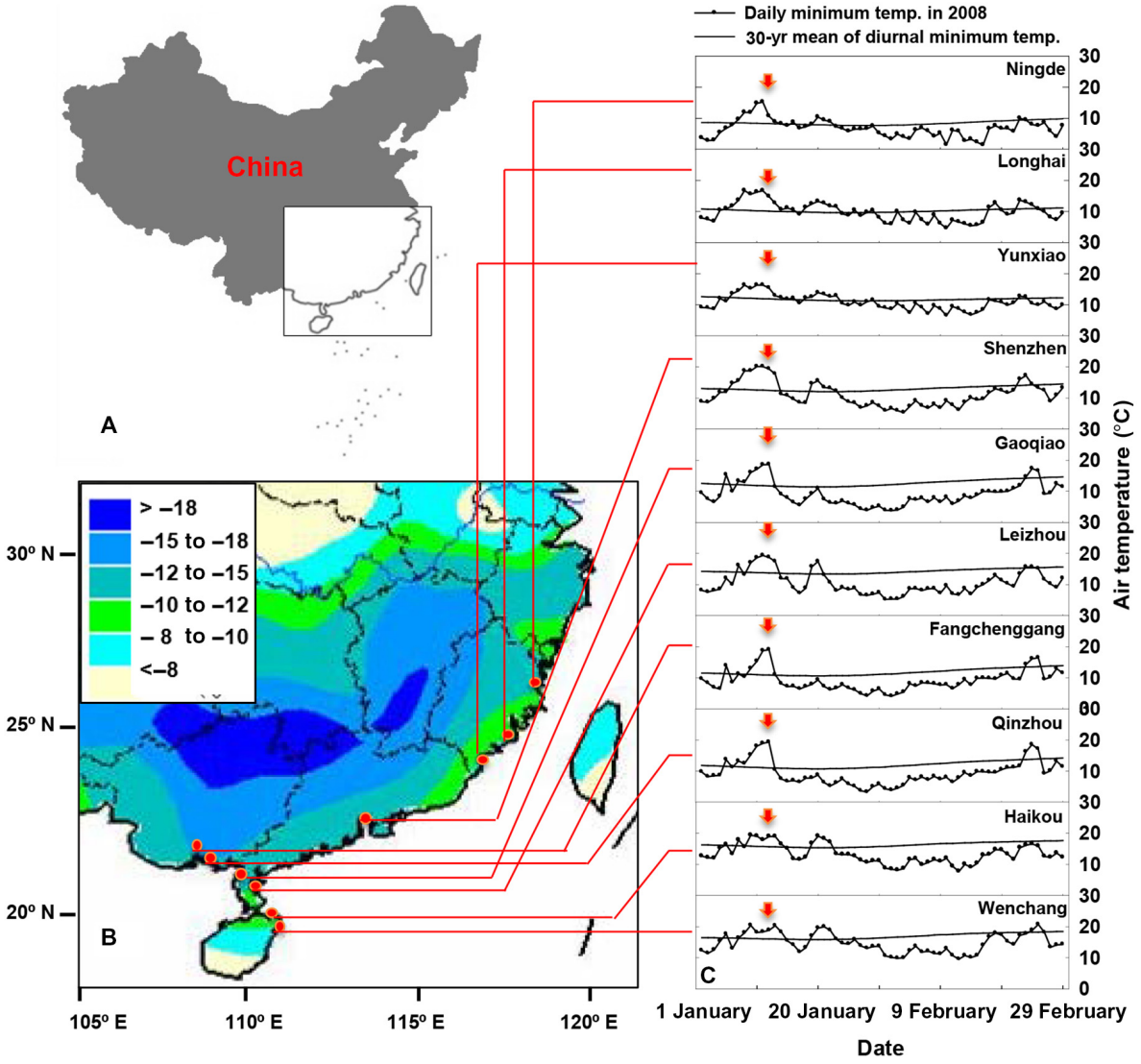


Fig. 1. (A) Map of the study area in China; (B) map of study sites and the minimum temperature anomaly (°C) during the chilling event relative to the 10-yr average (from China Meteorological Data Sharing Service System); (C) daily minimum air temperature (°C) data for each study site during the 2008 chilling event. Red arrows indicate the beginning of the chilling event.

combination of the following three factors: (1) Mangrove species diversity is comparatively high; (2) winter air temperature extremes, rather than just means, are particularly cold and play an important ecological role; and (3) due to afforestation and restoration efforts, several species of non-native mangroves have been introduced beyond their natural range limits. Hence, from a global perspective, extreme winter temperature events in China, like the one examined here, provide valuable opportunities to advance understanding of mangrove tolerance of freezing and chilling temperatures.

Methods

Study sites and timing of measurements

This study was conducted at 10 sites that span a latitudinal gradient in southern China (Fig. 1). From north to south, the 10 sites were (1–3)

Ningde, Longhai, and Yunxiao in Fujian Province; (4–6) Shenzhen, Leizhou, and Gaoqiao in Guangdong Province; (7–8) Qinzhou and Fangchenggang in Guangxi Province; and (9–10) Haikou and Wenchang in Hainan Province (Table 1, Fig. 1). At each site, four 10 × 10 m plots (i.e., four 100-m^2 plots) were randomly selected and established for subsequent sampling. Plots within a site had similar community composition, and the minimum distance between plots was 100 m. During data analyses, the four 100-m^2 plots at each site were considered replicates.

The chilling event that prompted this study occurred between 13 January and 20 February 2008 (Fig. 1). Our first survey began on 10 March 2008, approximately one month following the event. A second "recovery" survey was made near the end of the first post-chilling event growing season, between 15 November and 30 November 2008 (i.e., approximately nine months following the event).

Air temperature and tidal data

Air temperature data were obtained from the China Meteorological Data Sharing Service System (http://data.cma.cn/). For each site, we determined the following long-term air temperature-focused metrics: (1) mean annual air temperature (1981–2010); (2) mean annual minimum air temperature (1981–2010); and (3) absolute minimum air temperature (1954–2003, with the exception of Ningde, data were only available for the previous 12 yr). We also calculated a "diurnal anomaly of mean air temperature" metric, which indicates the anomaly in mean daily air temperatures during the chilling event (i.e., 10 January–20 February 2008) relative to the mean daily air temperatures for the same portion of the year (i.e., 10 January–20 February) over a 30-yr period (1981–2010). Tidal data were obtained from the 2008 tide tables (China Oceanic Information Network 2007) and used to calculate the mean tidal range for each of the 10 sites.

Focal mangrove species

A total of 12 mangrove species were encountered within the boundaries of all of the 100-m^2 plots present at the 10 study sites. One of these species, *Sonneratia apetala*, is a non-native species that was introduced to China from Bangladesh in 1985. The other 11 species include *Kandelia obovata*, *Aegiceras corniculatum*, *Avicennia marina*, *Bruguiera gymnorrhiza*, *Bruguiera sexangula*, *B. sexangula* var. *rhynchopetala*, *Rhizophora stylosa*, *Rhizophora apiculata*, *Sonneratia caseolaris*, *Sonneratia* ×*gulngai*, and *Sonneratia alba*. These latter 11 species are all native to China; however, their natural distributions in China greatly differ. For

Table 1. Latitude, temperature, and tidal characteristics for each of the 10 mangrove study sites.

Sites	Latitude (N)	Mean annual temp. (°C)	Mean annual min. temp. (°C)	Extreme low temp.† (°C)	Tide type‡	Extreme low temp. during the chilling event (°C)	Total ebb tide period at night during the chilling event§ (h)	Mean tidal range during the chilling event (m)
Ningde	26°41′	19.0	4.9	0.2	RST	1.4	294	5.6
Longhai	24°26′	21.0	4.7	2.0	RST	4.6	270	4.4
Yunxiao	23°54′	21.2	6.6	3.7	RST	6.5	255	2.7
Shenzhen	22°32′	22.5	4.6	0.2	IST	5.3	245	2.0
Gaoqiao	21°34′	23.0	4.5	1.5	MDT	5.2	295	3.8
Leizhou	21°00′	23.0	6.2	2.7	IST	3.8	242	3.0
Fangchenggang	21°28′	22.5	1.4	2.9	RDT	4.1	292	3.1
Qinzhou	21°43′	22.0	ND	−1.8	IDT	3.3	245	2.6
Haikou	19°54′	23.8	8.3	2.7	IDT	7.7	217	1.7
Wenchang	19°34′	24.0	9.2	5.0	IDT	9.5	222	1.3

Note: ND, no data.

† Extreme low temp. is the absolute minimum air temperature recorded between 1954 and 2003 with the exception of Ningde, where extreme low temp. is the absolute minimum air temperature recorded during the last 12 yr.

‡ Tide types are abbreviated as follows: RST, regular semi-diurnal tide; IST, irregular semi-diurnal tide; MDT, mixed diurnal tide; RDT, regular diurnal tide; IDT, irregular diurnal tide.

§ Ebb tide period at night during the chilling event is the ebb tide period from 6:00 p.m. to 5:00 a.m. from 10 January to 20 February 2008.

afforestation purposes, some of these species have even been introduced to areas north of their natural range limits. Hence, at each site, we assigned a code to each species, as shown in Appendix S1, to indicate whether a species was within its natural range (Group N, N for native species) or outside of and north of its natural range (Group O, O for non-native species outside of natural range). To quantify the northward position of non-native individuals relative to their natural distribution, we calculated a site-level "latitude increase" metric, which represents the position of a mangrove relative to its natural range limit. Positive latitude increase values reflect how far north a non-native species has been planted beyond its natural range.

Plant chilling damage and recovery measurements

Our measurements of mangrove damage and recovery focused on metrics that are indicative of physiological stress following chilling and freezing temperature extremes (Kao et al. 2004, Wang et al. 2011, Cook-Patton et al. 2015, Lovelock et al. 2016). Following extreme freezing or chilling events, defoliation of mangrove trees is common, which can lead to decreased growth, reproduction, and fitness (Tong et al. 2003, Ellis et al. 2006, Stuart et al. 2007, Wang et al. 2011). Leaf *Fv*/*Fm* values are a valuable leaf health index, and leaf *Fv*/*Fm* values lower than 0.8 are typically indicative of environmental stress (Björkman and Demmig 1987, Cook-Patton et al. 2015). Here, we used defoliation and leaf *Fv*/*Fm* values to investigate variability in mangrove species' responses to chilling temperature extremes.

Prior to the post-chilling event measurements, we took photographs of chilling damage to mangrove branches, leaves, and canopies (Figs. 2, 3). For each mangrove species present within each 100-m^2 plot at each site, we selected one or two trees of similar age, height, and growth status for



Fig. 2. Photographs illustrating freeze damage to mangrove species in China following the 2008 chilling event. (A–D) are native species: (A) *Bruguiera gymnorrhiza* in Gaoqiao; (B) *Avicennia marina* in Gaoqiao; (C) *Sonneratia caseolaris* in Wenchang; and (D) *Sonneratia alba* in Wenchang. (E–J) are non-native species: (E) *Rhizophora stylosa* in Longhai; (F) *Sonneratia apetala* in Shenzhen; (G) *S. caseolaris* in Haikou; (H) *S. caseolaris* in Shenzhen; (I) *S. apetala* in Leizhou; and (J) *S. apetala* in Qinzhou.

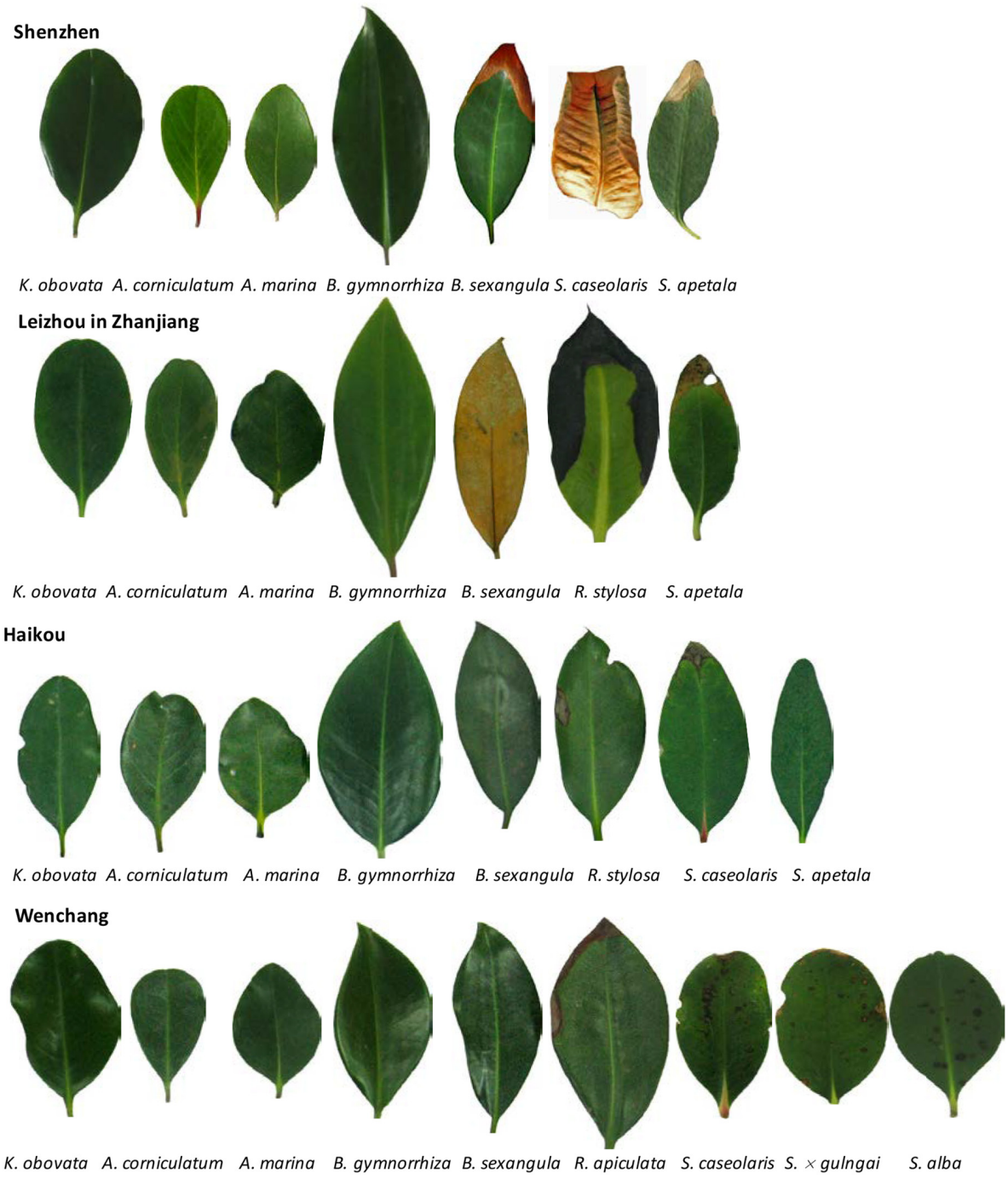


Fig. 3. Photographs of chilling temperature-induced damage to leaves of different mangrove species in Shenzhen, Leizhou, Haikou, and Wenchang study sites. See Table 2 for full species names.

plant measurements. For each of the selected trees, we quantified percent defoliation on 10 branches. For each branch, the defoliation percentage was calculated as the ratio of the number of defoliated leaves relative to the number of total leaves on a given branch. Recent leaf scars were counted as defoliated leaves due to the chilling event. For each of the trees selected for

measurement, we also took photographs of mature leaf browning.

In addition to leaf defoliation, leaf fluorescence parameters were also measured as an index of leaf stress. For three damaged and three healthy mature leaves on each of the selected trees, we measured fluorescence parameters using a portable fluorometer (PAM-2100; Walz, Effeltrich, Germany). Leaves were placed in the dark for 20 min before measuring dark adaptation fluorescence, including minimum (*Fo*) and maximum (*Fm*) fluorescence. The maximum steady-state photochemical efficiency of PSII was calculated as *Fv*/*Fm*, where $Fv = Fm - Fo$ (Krause and Weis 1991). In addition to the March 2008 measurements, the same fluorescence measurements were recorded in the same sample plots in Longhai and Wenchang approximately nine months later in November 2008.

Data analyses

For each of the 10 sites, we used the plot-level data (i.e., data from the four 100-m^2 plot replicates at each site) to calculate site-level means and standard errors (SE) for defoliation and leaf *Fv*/*Fm*. We used simple linear regression analyses to characterize the bivariate relationships between (1) latitude increase in non-native species and mangrove defoliation; (2) latitude increase in non-native species and leaf *Fv*/*Fm* values; (3) extreme minimum air temperature and species-specific leaf defoliation; (4) mangrove defoliation and various temperature and tidal condition metrics, for native and non-native species separately; and (5) mangrove leaf *Fv*/*Fm* and various temperature and tidal condition metrics, for native and non-native species separately. Analysis of covariance (ANCOVA) was used to test whether defoliation percentages and leaf *Fv*/*Fm* values differed between the native and non-native species among sites. Stepwise regression models were used to quantify the relationships between leaf damage variables (i.e., defoliation percentage and *Fv*/*Fm*) and environmental factors for native and non-native mangrove species. Analysis of variance (ANOVA) was used to compare leaf *Fv*/*Fm* values between the two measurement times at the Longhai and Wenchang study sites. All statistical analyses were conducted using SPSS17.0 (SPSS, Chicago, Illinois, USA).

Results

The 2008 chilling event caused extensive damage to mangroves along the coastline of subtropical China. Species from the *Sonneratia*, *Rhizophora*, and *Bruguiera* genera were sensitive to the chilling temperatures (Figs. 2, 3). *Sonneratia* species were the most sensitive to chilling temperatures and showed significant defoliation, even within their natural range in Wenchang (Table 2). Outside of their natural ranges, the introduced *Sonneratia apetala* performed better than the introduced *Sonneratia caseolaris*, which was totally defoliated and, in some cases, killed by the chilling temperatures in Shenzhen, Guangdong Province (Figs. 2, 3). In Haikou, Shenzhen, and Leizhou, *S. apetala* plantations were partly defoliated; however, they were totally dead in two sites in Guangxi Province (i.e., the Fangchenggang and Qinzhou sites; Table 2, Fig. 2). *Rhizophora* and *Bruguiera* species were partly defoliated or browning on leaf edges, even within their natural ranges (Figs. 2, 3). *Avicennia marina* is a widely distributed freeze-tolerant species whose leaves were only partly damaged via leaf browning (Table 2, Fig. 2). The damage to *Kandelia obovata* and *Aegiceras corniculatum* was even less than for *A. marina*, even though the native ranges of these species are within the same latitude.

For most species, there was a significant relationship between defoliation percentage and extreme minimum air temperatures during the chilling event (Appendix S2). For both non-native and native species, temperature metrics were correlated with defoliation and leaf *Fv*/*Fm* (Table 3). However, for some species, defoliation percentages were higher in southern sites compared to northern sites. For example, *A. marina* in Leizhou and Qinzhou had 20–24% defoliation, whereas no leaf fall at all was recorded for more northern sites in Fujian Province (Table 2; Appendix S2). Defoliation of *Bruguiera gymnorrhiza*, *Bruguiera sexangula*, and *Rhizophora stylosa* was also higher in certain central sites compared to more northern sites (Table 2; Appendix S2). Similar patterns were found in the non-native species *S. apetala*, which was seriously damaged and/or killed in sites within Guangdong and Guangxi provinces but less damaged in more northern sites (Table 2; Appendix S2). When comparing the trends of defoliation between the native and non-native species groups in relation

Table 2. Percent defoliation of mangrove species at each site following the 2008 chilling event.

Species	Ningde	Longhai	Yunxiao	Shenzhen	Gaoqiao	Leizhou	Fangchenggang	Qinzhou	Haikou	Wenchang
Kandelia obovata	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Aegiceras corniculatum	—	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Avicennia marina	—	**0**	**0**	**0**	**ND**	**24.1 ± 3.6**	**ND**	**20.0 ± 4.2**	**0**	**0**
Bruguiera gymnorrhiza	—	11.5 ± 6.1	**0**	**0**	**25.0 ± 5.7**	—	**ND**	**15.0 ± 1.5**	**0**	**0**
Bruguiera sexangula	—	35.1 ± 8.3	—	65.3 ± 4.8	—	100 ± 0.0	—	—	**0**	**0**
Bruguiera sexangula var. *rhynchopetala*	—	—	—	—	—	—	—	—	**0**	—
Rhizophora stylosa	—	30.2 ± 9.9	—	—	**19.2 ± 9.2**	**64.0 ± 9.0**	—	**100 ± 0.0**	**0**	—
Rhizophora apiculata	—	—	—	—	—	—	—	—	—	**40.1 ± 4.0**
Sonneratia caseolaris	—	—	—	100 ± 0.0	—	—	—	—	40.6 ± 9.4	**54.2 ± 4.2**
Sonneratia × *gulngai*	—	—	—	—	—	—	—	—	52.2 ± 4.3	**19.0 ± 13.5**
Sonneratia alba	—	—	—	—	—	—	—	—	—	**84.0 ± 2.5**
Sonneratia apetala	—	24.4 ± 10.7	—	44.5 ± 8.6	52.2 ± 4.0	56.9 ± 2.9	100	100	25.4 ± 3.1	—

Notes: A dash (—) indicates that a species is not present at a site. Boldface values indicate a native species (i.e., within its natural range). A value without boldface indicates a non-native species (i.e., a species that has been planted outside of its natural range). Data were partly published in Chen et al. (2010).

to changes in climatic and tidal characteristics, we found that the non-native species suffered more damage than the native species (Appendix S3).

For non-native species, there was not a significant relationship between latitude increase and defoliation (Fig. 4A), but there was a significant negative relationship between latitude increase and leaf *Fv*/*Fm* (Fig. 4B). The slope of the equation in Fig. 4B indicates that a ~0.05 decrease in leaf *Fv*/*Fm* occurs for each degree of latitude that a species is moved beyond its natural range limit. In addition to latitude, leaf *Fv*/*Fm* was negatively related to various temperature and tidal metrics (Appendix S4).

Table 3. Stepwise regression results from analyses of the relationships between leaf damage variables (i.e., defoliation percentage and *Fv*/*Fm*) and environmental factors for native (Group N) and non-native (Group O) mangrove species.

Dependent variables	Species groups	Variables	Unstandardized coefficients	SE	*t*	*P*	df	R^2
Defoliation percentages	Group N	Anomaly temp.†	−3.207	1.072	−2.991	0.003	128	0.066
		Constant	−20.988	10.600	−1.980	0.050		
	Group O	Tidal range‡	−21.101	4.778	−4.416	<0.001	41	0.611
		Extreme low temp.§	−19.005	3.092	−6.147	<0.001		
		Anomaly temp.	−3.715	2.051	−1.811	0.078		
		Constant	181.654	39.512	4.597	<0.001		
Fv/*Fm* values	Group N	Tidal range	−0.024	0.003	−7.165	<0.001	109	0.322
		Constant	0.852	0.009	99.086	<0.001		
	Group O	Anomaly temp.	−0.053	0.010	−5.285	<0.001	35	0.451
		Constant	0.237	0.092	2.561	0.015		

† Anomaly temp.: diurnal anomaly of mean air temperature.
‡ Tidal range: mean tidal range during the chilling event.
§ Extreme low temp.: extreme low air temperature.

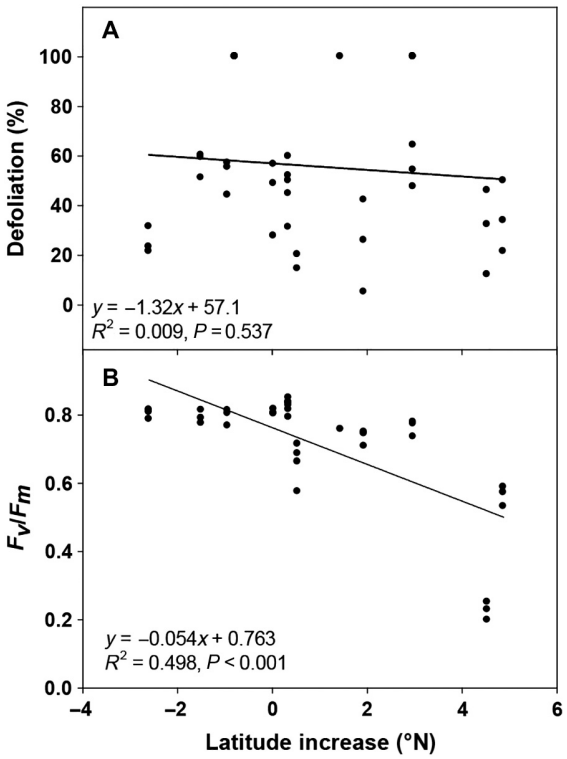


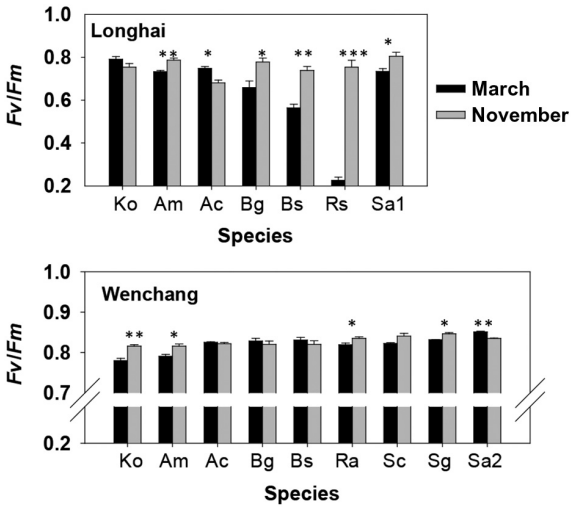
Fig. 4. Damage to non-native mangrove species following the 2008 chilling event. Relationships between (A) percent defoliation of non-native species and latitude increase and (B) leaf *Fv*/*Fm* values of non-native species and latitude increase. Latitude increase indicates the position of a mangrove relative to its natural range limit (i.e., positive values indicate how far north a non-native species has been planted beyond its natural range).

Nine months after the chilling event, mangrove leaves, both at the northern Longhai site and at the southern Wenchang site, showed little damage and remarkable recovery. In Longhai, leaf *Fv*/*Fm* values of almost all mangrove species in November 2008 were significantly higher than those in March 2008, except for *K. obovata* and *A. corniculatum* (Fig. 5). *Rhizophora apiculata* and *Sonneratia ×gulngai,* which were both seriously damaged in March 2008, had much higher leaf *Fv*/*Fm* values after nine months (Fig. 5). Although *K. obovata* and *A. marina* were not damaged by the chilling event, these two species had even higher leaf *Fv*/*Fm* values after the nine-month period. In Wenchang, the values for almost all species in November 2008 were similar to those in March 2008.

Discussion

Mangrove species' responses to chilling temperature extremes in China

We found that variation in cold sensitivity, as measured by defoliation and *Fv*/*Fm* values, was positively related to temperature during the chilling event and to the poleward distribution of each species. For example, *Kandelia obovata* and *Aegiceras corniculatum*, the mangrove species with the most northern distribution, were the species that were most tolerant of the chilling temperatures. In contrast, *Avicennia marina* and *Rhizophora*



	Longhai		Wenchang	
Sites	**df**	***F*-value**	**df**	***F*-value**
Species	6	61.076***	8	18.414***
Time	1	159.831***	1	10.565**
Species × Time	6	58.736***	8	6.705***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Fig. 5. Maximum photochemical efficiency of PSII (ΦPSII; mean ± SE *Fv*/*Fm*) of mangrove species at two study sites (Longhai and Wenchang) following the 2008 chilling event. March and November measurements were taken approximately one and nine months after the event, respectively. Univariate ANOVA results are also shown. Ko, *Kandelia obovata*; Am, *Avicennia marina*; Ac, *Aegiceras corniculatum*; Bg, *Bruguiera gymnorrhiza*; Bs, *Bruguiera sexangula*; Rs, *Rhizophora stylosa*; Ra, *Rhizophora apiculata*; Sc, *Sonneratia caseolaris*; Sg, *Sonneratia × gulngai*; Sa1, *Sonneratia apetala*; Sa2, *Sonneratia alba*.

stylosa in Leizhou, *Bruguiera gymnorrhiza* and *R. stylosa* in Gaoqiao, and *A. marina* and *B. gymnorrhiza* in Qinzhou all suffered various forms of damage from the chilling temperature extremes, even within their natural distribution. Our results indicate that species in the *Sonneratia* genus are highly sensitive to chilling temperatures. *Sonneratia* individuals were seriously injured by the chilling temperatures, even within their natural range at the Wenchang site.

Non-native species that were transplanted northward of their natural range limits (e.g., *Sonneratia caseolaris* in Shenzhen and *Sonneratia apetala* in Fangchenggang) suffered serious damage or died after the chilling event. The leaf health index of these non-native species was lower than for native species, indicating that chilling temperatures resulted in a greater degree of leaf damage and reduced leaf photosynthesis (Fig. 4). Diurnal anomalies of mean air temperature, extreme low temperature, and tidal range were correlated with non-native species' defoliation during the chilling event. However, for native species, only the diurnal anomaly of mean air temperature significantly aggravated the damage to mangrove leaves.

Our results show that mangroves in southern sites suffered greater injury from the chilling event compared to those in northern sites, which is similar to the findings in North America. Mangrove individuals from southern coastal reaches of North America are less tolerant of freezing and chilling temperatures than mangroves in more northern coastal reaches (Markley et al. 1982, Madrid et al. 2014, Cook-Patton et al. 2015). Apart from the adaptive evolution of the species at the northern edges, chilling intensity relative to normal conditions may be another driver for the patterns observed in our study. During the chilling event, climatic parameters, such as diurnal mean air temperature, varied among sites (Fig. 1), which, in turn, resulted in variability of damage along the latitudinal gradient. In northern sites (e.g., Ningde, Longhai, and Yunxiao), the mean minimum temperature decreased about 8–10°C from normal; however, in some southern sites (e.g., Zhanjiang, Qinzhou, Haikou, and Wenchang), the mean minimum temperature was 10–12°C lower than normal (Fig. 1B), which led to greater defoliation. Species with higher chilling resistance (e.g., *K. obovata*, *A. corniculatum*, and *A. marina*) showed no defoliation as a consequence of their higher tolerance of low temperatures (Chen et al. 2010). The patterns of cold damage were strongly correlated with the geographic variability of chilling intensity, as well as species-specific tolerances to cold stress.

Sensitivity classes for communicating species' tolerance of winter temperature extremes

For communication purposes, mangrove and other plant species are often grouped according to their sensitivity to freezing and chilling temperatures (Clough 1992, Daly et al. 2012, Lovelock et al. 2016, Parker and Abatzoglou 2016). For China, Yang and Lin (1998) classified mangrove species into three cold sensitivity classes according to the poleward position of their natural range limits as well as the electrolyte leakage of mature leaves during chilling temperatures (Table 4). Species-specific half-lethal low temperatures were recorded, and the sensitivity to freezing temperatures was expressed as a half-lethal temperature (LT50, °C; Yang and Lin 1998). The LT50s for mangroves in the High (H), Medium (M), and Low (L) cold sensitivity classes were identified as follows: (1) warmer than −4°C; (2) between −6° and −4°C; and (3) lower than −6°C, respectively.

In a similar manner, we used our defoliation and *Fv*/*Fm* results to group the 12 mangrove species into High (H), Medium (M), and Low (L)

Table 4. Cold sensitivity classes for 12 mangrove species in China.

Species	Cold sensitivity classes	
	Yang and Lin (1998)	Present study
K. obovata	L	L
A. corniculatum	L	L
A. marina	—	L
B. gymnorrhiza	L	L
B. sexangula	L	M
B. sexangula var. *rhynchopetala*	L	M
R. stylosa	M	M
R. apiculata	M	H
S. caseolaris	H	H
S. ×gulngai	—	H
S. alba	H	H
S. apetala	—	M

Notes: H, M, and L refer to High, Medium, and Low cold sensitivity classes, respectively. A dash (—) indicates that a species was not present and not evaluated in that study. See Table 2 for full species names.

cold sensitivity classes. Most species were classified in the same grouping as in Yang and Lin (1998); however, our classification, based upon the results from this study, was different for the following three species: *Bruguiera sexangula*, *Bruguiera sexangula* var. *rhynchopetala*, and *Rhizophora apiculata*. All three of these species were defoliated within their natural ranges, as well as in northern sites outside of their natural ranges. Hence, we placed these three species in the Medium cold sensitivity class. Based on observations and measurements of these same species nine months after the chilling event, the same conclusions were reached. These classifications based on our regional-scale comparisons of species-specific mangrove responses to a chilling temperature extreme should be particularly useful for scientists and resource managers interested in gauging species-specific sensitivity to chilling. A common garden experimental design (Liu et al. 2016, 2017) could be a valuable approach for advancing our understanding and refining the placement of species in cold sensitivity classes.

Tidal modulation of the effects of winter temperature extremes

In addition to climatic disturbances, mangroves are also subject to hydrological disturbances with different duration, frequency, and intensity. Prior laboratory experiments (Chen et al. 2012) and field observations (Wang et al. 2011) have shown that tidal conditions (e.g., tidal range and inundation time) can alleviate the effects of low air temperature extremes on mangroves. The warming effect of tidewater can increase mangrove survival and growth during and following winter temperature extremes (Wang et al. 2011). In this study, the modulating effects of tidal inundation on chilling damage were significant (Table 3). Although low air temperature is a limiting factor that governs mangrove distribution, our results suggest that the modulating effects of hydrological factors (e.g., tidal range and ebb tide period at night) should also be considered in analyses of chilling effects on mangroves and other estuarine organisms.

How does the range limit of mangroves in China compare to others across the globe?

Compared to temperature-controlled mangrove distributional range limits in the Atlantic East Pacific biogeographical region (i.e., North America, South America, and western Africa; Duke et al. 1998), mangrove species diversity in China is relatively high with a total of 24 true mangrove species and 12 mangrove associates (Wang and Wang 2007). For comparison, only three mangrove species are common near the northern range limit of mangroves in eastern North America (Tomlinson 1986, Ross et al. 2009). In China, species-specific sensitivity to extreme minimum air temperatures is variable, and there is a decrease in species richness from low latitudes (~18° N) to high latitudes (~28° N; Lin 1999).

Like in China, winter air temperature regimes also govern the poleward distribution, abundance, and species richness of mangroves in eastern Australia, New Zealand, southern Africa, western South America, western North America, and eastern North America (Duke 1990, Woodroffe and Grindrod 1991, Saenger 2002, Quisthoudt et al. 2012, Soares et al. 2012, Osland et al. 2013, Cavanaugh et al. 2014, 2015, Saintilan et al. 2014). However, winter air temperature regimes and the intensity of extremes within these range limits are highly variable, which has important ecophysiological ramifications for mangroves (Lovelock et al. 2016, Osland et al. 2017*b*). For example, winter air temperature extremes play a more important role in eastern North America than in eastern Australia, which results in different physiological adaptations and sensitivity to freezing (Stuart et al. 2007). The mangrove range limit in China is most similar to the mangrove range limit in eastern North America in that air temperature extremes, rather than means, can be particularly intense and ecologically important in both of these regions (Osland et al. 2017*b*).

The presence of non-native mangrove species (i.e., species planted outside of their natural range) also makes the mangrove range limit in China particularly interesting. Like many regions of the world, the historical rate of mangrove loss in China has been high due to conversion of mangroves to other land uses (Wang and Wang 2007). To counter mangrove losses, mangrove afforestation efforts have been implemented in many parts of China (Chen et al. 2009). During afforestation, non-native mangrove species are sometimes used, which has resulted in the introduction of some species to areas that are north of, and colder than, their natural range. For example, *K. obovata*, the

most widely distributed and most cold-resistant mangrove species in China, was successfully introduced one degree north of its natural range limit in the 1950s; it was transplanted to Yueqing in Zhejiang Province (28°20′ N) from its northernmost distribution site in Fuding, Fujian Province (27°17′ N; Lin 1999). Other species with high growth rates and an aesthetically pleasing appearance, such as *B. gymnorrhiza*, *B. sexangula*, *R. stylosa,* and *S. caseolaris*, have also been transplanted to sites north of their natural range (Lin 1999). *Sonneratia apetala* was introduced from Bangladesh and has been used during mangrove afforestation in many parts of China (Chen et al. 2009). Many of the introduced mangrove species in China come from more tropical locations with warmer winter air temperature regimes; hence, these non-native species are often more sensitive to freezing and chilling than species within their natural range. Freeze damage and mortality could affect the outcome of mangrove afforestation, and studies like this one can be used to guide species selections made during mangrove afforestation and restoration efforts.

Conclusions

The 2008 chilling event caused remarkable damage to mangroves in southern China. Our findings show that there was a high degree of geographical and species-specific variability in mangrove defoliation and leaf injury. Certain species were more sensitive to chilling temperature extremes. Whereas species in the *Sonneratia* genus were the most cold sensitive, *Kandelia obovata*, *Aegiceras corniculatum*, and *Avicennia marina* were tolerant of the chilling temperature extremes. Non-native species introduced north of their natural range suffered more serious injury than native species within their natural range. However, at the leaf ecophysiological level, both the native and non-native mangrove species recovered after nine months. Our results provide valuable information which can be used to better understand the effects of climate change on mangroves and better inform the selection of appropriate mangrove species for afforestation. Climate change is expected to alter the frequency and intensity of climate extremes, which will greatly affect mangrove forests. By the end of this century, less frequent and less intense freeze events are expected to enable the poleward migration of mangroves. Within the context of climate change, our findings provide a foundation for better understanding and preparing for the species-specific responses of mangroves to changing winter air temperature regimes.

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Literature Cited

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52–66.

Björkman, O., and B. Demmig. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 k among vascular plants of diverse origins. Planta 170:489–504.

Boucek, R. E., E. E. Gaiser, H. Liu, and S. Rehage. 2016. A review of subtropical community resistance and resilience to extreme cold spells. Ecosphere 7:e01455.

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

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

Chen, L., X. Du, L. Lu, S. Zheng, and S. Yang. 2012. Synergistic effects of low temperature in winter and ebb tide at night on *Sonneratia apetala* seedlings growth and key eco-physiological traits. Chinese Journal of Applied Ecology 23:953–958 [In Chinese with English Abstract.].

Chen, L., W. Wang, Y. Zhang, and G. Lin. 2009. Recent progresses in mangrove conservation, restoration and research in China. Journal of Plant Ecology 2:45–54.

Chen, L., et al. 2010. Damage to mangroves from extreme cold in early 2008 in southern China. Journal of Plant Ecology 34:186–194 [In Chinese with English Abstract.].

China Oceanic Information Network. 2007. 2008 tide tables. China Ocean Press, Beijing, China.

Clough, B. F. 1992. Primary productivity and growth of mangrove forests. Pages 225–249 *in* A. I. Robertson and D. M. Alongi, editors. Tropical mangrove ecosystems. American Geophysical Union, Washington, D.C., USA.

Coldren, G. A., and C. E. Proffitt. 2017. Mangrove seedling freeze tolerance depends on salt marsh presence, species, salinity, and age. Hydrobiologia. https://doi.org/10.1007/s10750-017-3175-6:1-13

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

Daly, C., M. P. Widrlechner, M. D. Halbleib, J. I. Smith, and W. P. Gibson. 2012. Development of a new USDA plant hardiness zone map for the United States. Journal of Applied Meteorology and Climatology 51:242–264.

Duke, N. C. 1990. Phenological trends with latitude in the mangrove tree *Avicennia marina*. Journal of Ecology 78:113–133.

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

Ellis, W. L., J. W. Bowles, A. A. Erickson, N. Stafford, S. S. Bell, and M. Thomas. 2006. Alteration of the chemical composition of mangrove (*Laguncularia racemosa*) leaf litter fall by freeze damage. Estuarine, Coastal and Shelf Science 68:363–371.

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

Glick, P., B. A. Stein, and N. A. Edelson, editors. 2011. Scanning the conservation horizon: a guide to climate change vulnerability assessment. National Wildlife Federation, Washington, D.C., USA.

Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22:534–543.

Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. Ecology 95:2646–2656.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment 5:365–374.

Kao, W. Y., S. C. Shih, and T. T. Tsai. 2004. Sensitivity to chilling temperatures and distribution differ in the mangrove species *Kandelia candel* and *Avicennia marina*. Tree Physiology 24:859–864.

Kozlowski, T. T., and S. G. Pallardy. 1997. Growth control in woody plants. Academic Press, San Diego, California, USA.

Krause, G. H., and E. Weis. 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annual Review of Plant Physiology and Plant Molecular Biology 42:313–349.

Krauss, K. W., C. E. Lovelock, K. L. McKee, L. López-Hoffman, S. M. L. Ewe, and W. P. Sousa. 2008. Environmental drivers in mangrove establishment and early development: a review. Aquatic Botany 89:105–127.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Springer-Verlag, Berlin, Germany.

Lin, P. 1999. Mangrove ecosystem in China. Science Press, Beijing, China.

Liu, W., K. Maung-Douglass, D. R. Strong, S. C. Pennings, and Y. Zhang. 2016. Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. Journal of Ecology 104:173–181.

Liu, W., D. R. Strong, S. C. Pennings, and Y. Zhang. 2017. Provenance-by-environment interaction of reproductive traits in the invasion of *Spartina alterniflora* in China. Ecology 98:1591–1599.

Lonard, R. I., and F. W. Judd. 1991. Comparison of the effects of the severe freezes of 1983 and 1989 on native woody plants in the Lower Rio Grande Valley, Texas. Southwestern Naturalist 36:213–217.

Lovelock, C. E., K. W. Krauss, M. J. Osland, R. Reef, and M. C. Ball. 2016. The physiology of mangrove trees with changing climate. Pages 149–179 *in* G. Goldstein and L. S. Santiago, editors. Tropical tree physiology: adaptations and responses in a changing environment. Springer, New York, New York, USA.

Lugo, A. E., and C. Patterson-Zucca. 1977. The impact of low temperature stress on mangrove structure and growth. Tropical Ecology 18:149–161.

Madrid, E. N., A. R. Armitage, and J. López-Portillo. 2014. *Avicennia germinans* (black mangrove) vessel architecture is linked to chilling and salinity tolerance in the Gulf of Mexico. Frontiers in Plant Science 5:503.

Markley, J. L., C. McMillan, and G. A. Thompson Jr. 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. Canadian Journal of Botany 60:2704–2715.

Osland, M. J., R. H. Day, A. S. From, M. L. McCoy, J. L. McLeod, and J. J. Kelleway. 2015. Life stage influences the resistance and resilience of black mangrove forests to winter climate extremes. Ecosphere 6:1–15.

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

Osland, M. J., N. Enwright, R. H. Day, and T. W. Doyle. 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., et al. 2017*b*. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. Ecological Monographs. https://doi.org/10.1002/ecm.1248

Parker, L. E., and J. T. Abatzoglou. 2016. Projected changes in cold hardiness zones and suitable overwinter ranges of perennial crops over the United States. Environmental Research Letters 11:034001.

Pickens, C. N., and M. W. Hester. 2011. Temperature tolerance of early life history stages of black mangrove *Avicennia germinans*: implications for range expansion. Estuaries and Coasts 34:824–830.

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

Ross, M. S., P. R. Ruiz, J. S. Sah, and E. J. Hanan. 2009. Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida. Global Change Biology 15:1817–1832.

Saenger, P. 2002. Mangrove ecology, silviculture and conservation. Kluwer Academic, Dordrecht, The Netherlands.

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

Sakai, A., and W. Larcher. 1987. Frost survival of plants: responses and adaptation to freezing stress. Springer-Verlag, Berlin, Germany.

Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journal of Ecology 99:656–663.

Soares, M. L. G., G. C. D. Estrada, V. Fernandez, and M. M. P. Tognella. 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.

Stuart, S. A., B. Choat, K. C. Martin, N. M. Holbrook, and M. C. Ball. 2007. The role of freezing in setting the latitudinal limits of mangrove forests. New Phytology 173:576–583.

Tomlinson, P. B. 1986. The botany of mangroves. Cambridge University Press, Cambridge, UK.

Tong, Y. F., S. Y. Lee, and B. Morton. 2003. Effects of artificial defoliation on growth, reproduction and leaf chemistry of the mangrove *Kandelia candel*. Journal of Tropical Ecology 19:397–406.

Vergés, A., et al. 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.

Wang, W. Q., and M. Wang. 2007. The mangroves of China. Science Press, Beijing, China.

Wang, W. Q., S. Y. You, Y. B. Wang, L. Huang, and M. Wang. 2011. Influence of frost on nutrient resorption during leaf senescence in a mangrove at its latitudinal limit of distribution. Plant and Soil 342:105–115.

Woodroffe, C. D., and J. Grindrod. 1991. Mangrove biogeography: the role of quaternary environmental and sea-level change. Journal of Biogeography 18:479–492.

Woodward, F. I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge, UK.

Yang, S., and P. Lin. 1998. Ecological studies on the resistance and adaptation to cold of some tidal mangrove species in China. Acta Phytoecologica Sinica 22:60–67 [In Chinese with English Abstract.].

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