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Extremely low genetic diversity across mangrove taxa reflects past sea level changes and hints at poor future responses

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Abstract

The projected increases in sea levels are expected to affect coastal ecosystems. Tropical communities, anchored by mangrove trees and having experienced frequent past sea level changes, appear to be vibrant at present. However, any optimism about the resilience of these ecosystems is premature because the impact of past climate events may not be reflected in the current abundance. To assess the impact of historical sea level changes, we conducted an extensive genetic diversity survey on the Indo-Malayan coast, a hotspot with a large global mangrove distribution. A survey of 26 populations in six species reveals extremely low genome-wide nucleotide diversity and hence very small effective population sizes (N_e) in all populations. Whole-genome sequencing of three mangrove species further shows the decline in N_e to be strongly associated with the speed of past changes in sea level. We also used a recent series of flooding events in Yalong Bay, southern China, to test the robustness of mangroves to sea level changes in relation to their genetic diversity. The events resulted in the death of half of the mangrove trees in this area. Significantly, less genetically diverse mangrove species suffered much greater destruction. The dieback was accompanied by a drastic reduction in local invertebrate biodiversity. We thus predict that tropical coastal communities will be seriously endangered as the global sea level rises. Well-planned coastal development near mangrove forests will be essential to avert this crisis.

KEYWORDS
dieback, effective population size, genetic diversity, human disturbance, mangroves, sea level rise

1 | INTRODUCTION

Sea levels are projected to rise by one metre over the next century (IPCC, 2013), and coastal ecosystems are expected to bear the brunt

of this change. Mangroves, which anchor tropical coastal communities, are particularly vulnerable because they already occupy a niche that is on the extreme margin of the woody plant distribution. We and many others have studied the adaptability of major mangrove taxa as well as their evolutionary diversification (Guo et al., 2016; Urashi, Teshima, Minobe, Koizumi, & Inomata, 2013; Wee et al.,

2015; Xu, He, Guo, et al., 2017; Xu, He, Zhang, et al., 2017; Yang et al., 2017; Zhou et al., 2011). From the genomic perspective, adaptation of woody plants to this new environment has been an arduous process (Xu, He, Guo, et al., 2017), which may partially explain the existence of fewer than 80 mangrove species globally.

Mangroves are ecologically important for ameliorating the impact of flooding, supporting coastal food webs and sequestering carbon (Barbier et al., 2011). If mangroves vanish, many tropical ecosystems that depend on them may cease to exist. Large human populations live in low areas along tropical coastlines (Mcgranahan, Balk, & Anderson, 2007). The livelihoods of these people depend directly or indirectly on mangrove ecosystem services, the value of which has been estimated at US$194,000/hectare/year (Costanza et al., 2014). Human impact, however, has already resulted in mangrove deforestation at a rate of 1–2% per year (Duke et al., 2007). Climate change and its attendant change in sea levels exacerbate this trend. A 'world without mangroves' by 2080 (Duke et al., 2007) is thus an alarming possibility.

The presumed ability of mangroves to modify their environment (Krauss et al., 2014) and hence their capacity to mitigate the effects of flooding through vertical accretion of sediments (Lovelock et al., 2015; Mckee, Cahoon, & Feller, 2007) has been a source of optimism for their future survival. Even when sea levels change too drastically for soil accretion to keep pace, mangroves may survive by retreating into adjacent habitats (Doyle, Krauss, Conner, & From, 2010; Lovelock et al., 2015). Mangroves have survived many past catastrophic climate events, including sea level drops to 120–125 m lower than the present levels during the last glacial maximum as well as the subsequent rapid sea level rise (an average of more than one metre per century over 10,000 years) (Alongi, 2015). The paleo-geological records indicate that mangroves have largely adapted to changing sea levels, though some of them became locally extinct in regions where the coasts were submerged beyond a critical threshold (Alongi, 2015).

The impact of the rapid change in sea level in the last 20,000 years, however, is not discernible in the extant coastal ecosystems. Mangrove forests may have suffered great losses but became vibrant during the last 6,000 years when the sea levels have been relatively (and unusually) stable. This interval has coincided with the entire period of human civilization. Population-genetic data can provide a more comprehensive picture of the historic effect of climate change. We thus performed a large-scale genetic diversity survey across multiple species of mangroves and multiple populations on the Indo-Malayan coast. Furthermore, based on the genomic sequences we reported earlier (Xu, He, Zhang, et al., 2017), it is possible to evaluate changes in the effective population sizes of several species of mangroves over the past 100,000 years. Such an assessment of temporal change may be particularly informative in conjunction with data on sea level changes.

Finally, short-term changes in sea level that affect the tropical coastal ecosystems are increasingly observable. In the latter part of 2015, a massive mangrove dieback occurred across a 1,000-km front in northern Australia. Among the many possible causes was a month-long drop of 20 cm in local sea levels, likely caused by a strong El Nino (Duke et al., 2017). A smaller scale mangrove dieback was recorded in the Yalong Bay reserve (Hainan, China) between 2010 and 2012, brought about by a combination of natural and man-made causes and a concomitant water level rise. Because the genetic diversity of mangroves in Hainan has been extensively measured in the present study, it is possible to correlate past changes with current and future perturbations. This study is thus both a retrospective analysis and prospective inference of coastal communities anchored by mangroves.

2 | MATERIALS AND METHODS

2.1 | Sample collection, DNA extraction and sequencing

We collected population samples from six typical true mangrove species (*Sonneratia alba*, *Ceriops tagal*, *Avicennia marina*, *Rhizophora apiculata*, *Aegiceras corniculatum* and *Xylocarpus granatum*) in the Yalong Mangrove Reserve and neighbouring locations in Sanya between 2008 and 2009. We added samples from across the region, expanding coverage to 16 stands on the coasts of Hainan Island and Gulf of Thailand that were collected at the same time. Leaf material was sampled from 285, 300, 289, 158, 30 and 224 individuals from the six species. Sampled individuals were at least 15 m apart. Leaves were stored in plastic bags with silica gel before DNA extraction. For five of the six species (except *X. granatum*; see below), we followed the approach described in our earlier work (Zhou et al., 2011) to pool equal quantities of leaf material from each sample within each species to extract DNA. We amplified 62–94 genes from each pooled DNA sample and pooled the PCR products for sequencing on the Illumina GA-II/HiSeq 2000 platform (Illumina, San Diego, CA, USA). PCR primers were designed based on cDNA libraries or transcriptomes of *S. caseolaris*, *C. tagal*, *Av. marina*, *R. mangle* and *Ae. corniculatum* (Chen et al., 2015; Huang et al., 2012; Zhou et al., 2011). Starting with approximately 200 pairs of primers anchored in exons, we retained an average of 80 pairs, which yielded products between 500 and 1,500 bp long.

2.2 | SNP calling and genetic diversity analyses

Short reads were mapped to reference libraries using MAQ (Li, Ruan, & Durbin, 2008), and Single Nucleotide Polymorphisms (SNPs) were called as described in our earlier work (Guo et al., 2016). As previously described, the called SNPs were validated by sequencing randomly selected products using the Sanger method. The sequenced segments from *S. alba* were assigned to 101 gene segments, *C. tagal* to 102, *Av. marina* to 150, *R. apiculata* to 124 and *Ae. corniculatum* to 115. We employed an expectation-maximization algorithm (Bilmes, 1998; Dempster, Laird, & Rubin, 1977), which takes advantage of the linkage information among SNPs between paired reads to infer haplotypes and their frequencies for each segment. The 30 samples from *X. granatum* were sequenced using the Sanger method

in seven gene segments in a companion study (Guo et al., in submission). We used these sequences to estimate the nucleotide diversity (π) in regional populations following Nei's formula (Nei & Li, 1979). We also computed Wright's F statistic (F_{ST}) according to the formula $F_{ST} = 1 − \pi_{Within}/\pi_{Between}$, where $\pi_{Between}$ and π_{Within} represent the average number of pairwise differences between two individuals sampled from different populations ($\pi_{Between}$) or from the same population (π_{Within}), respectively.

2.3 │ Genome sequencing and PSMC analyses

The Pairwise Sequentially Markovian Coalescent (PSMC) method takes advantage of differences between two haploid genomes within an individual to infer historical changes in N_e. Each genome is divided into hundreds of segments, and the divergence level of each segment reflects the amount of time necessary for the two haploid segments to coalesce back to the common ancestor. This coalescence time is a function of the historical N_e, thus permitting the inference of time-dependent changes going backward in the evolutionary history.

Whole-genome assemblies of *R. apiculata* (Xu, He, Zhang, et al., 2017b), as well as of *Av. marina* and *S. alba* (He et al., in submission), are reported elsewhere. An efficient *de novo* assembly requires the selection of individuals with low heterozygosity for initial analyses. To mitigate any potential biases introduced by this procedure, we randomly collected and sequenced one individual from each species: *R. apiculata* from Sanya, China; *Av. marina* from Thongnian Bay, Thailand; and *S. alba* from Chaiya, Thailand. The extracted genomic DNA was sequenced using the Illumina HiSeq 2000 platform with 200-bp paired-end reads. Short reads from single *R. apiculata*, *Av. marina*, and *S. alba* individuals were mapped to reference genomes using BWA (Burrows-Wheeler Aligner) (Li & Durbin, 2009). Reads were filtered by removing potential PCR-duplicated, single-end mapped, and improperly paired mapped reads as per the GATK (Genome Analysis Toolkit) instructions (DePristo et al., 2011; Van der Auwera et al., 2013). Because the average coverage per individual was approximately 15X, we retained only sites with read depths greater than five and lower than 150. We ran the PSMC program (Li & Durbin, 2011) with the parameters -N25 −t15 -r5 -p "4 + 25*2 + 4 + 6″. The generation time was set to 20 years, and the mutation rate was set to 1.6×10^{-8}, 3.1×10^{-8} and 2.8×10^{-8} bp/site/generation for the three species (He et al., in submission).

2.4 │ Climate and mortality data collection

We surveyed mangrove forests throughout Yalong Bay in January 2012 after the dieback event. Mangrove trees were classified into four groups: healthy (all leaves were green and dense), subnormal (most leaves were green), ill (only a few leaves were green) and dead (all leaves were withered or trees were bare). We recorded the condition of individual trees from dominant mangrove species throughout the reserve. To determine the relationship between flooding and plant survival, we examined *C. tagal* trees, the species that was most severely affected, more carefully. We recorded the numbers of *C. tagal* trees that fell into each category according to the elevation along two transect lines (upstream and downstream) from the seaward to the landward margin. We also used publically available satellite images to assess the overall extent and geographical patterns of the dieback event. Climate (rainfall) data were collected from the Liudaoling climatological station in Yalong Bay and the Hedong station in Sanya (Fig. S1).

3 │ RESULTS

3.1 │ Extant genetic diversity in mangroves

To determine the current level of genetic diversity in mangroves, we collected and sequenced 26 population samples from six species of mangroves located in 16 areas along the coasts of Hainan Island and the Gulf of Thailand (Figure 1a, and Table S1). We sequenced 285 individual trees (101 gene segments, 59.6 Kb) from *S. alba*, 300 (102 gene segments, 76.6 Kb) from *C. tagal*, 289 (150 gene segments, 85.2 Kb) from *Av. marina*, 158 (124 gene segments, 65.2 Kb) from *R. apiculata*, 30 (7 gene segments, 6.1 Kb) from *X. granatum*, and 224 (115 gene segments, 57.3 Kb) from *Ae. corniculatum*. We observed markedly low genetic diversity in local populations of all six species (Figure 1b). The mean values of nucleotide diversity (π) were under 1.0×10^{-3} in most populations. While the populations of *Ae. corniculatum* have larger π values, they are also quite low in comparison with other woody plants (Figure 1b). Most notable is the Hainan population of *S. alba*, which is completely devoid of genetic variation, consistent with previous results (Zhou et al., 2011).

A low genetic diversity within populations may hide variation if there is differentiation among populations within a region. To test this, we calculated F_{ST}, the statistic that reflects the fraction of the overall regional polymorphism that is attributable to among-population divergence. $F_{ST} = 0$ implies no genetic differentiation between populations, while $F_{ST} = 1$ suggests that genetic diversity only exists between populations. As shown in Figure 1c, the F_{ST} values between populations within regions are very low. Even populations from different regions (Hainan and Gulf of Thailand being geographically distant) have low F_{ST} values (Figure 1c), which is analysed in detail in a companion paper (He et al., in submission). The low genetic diversity is thus a regional rather than a local phenomenon.

This low nucleotide polymorphism has two important implications. First, it may reflect possible severe reductions in mangrove population sizes as the sea levels changed greatly in the past. In this view, the low genetic diversity is the consequence of a species' inability to sustain a large population size when the sea level changes. Second, the low genetic diversity may also be a causal factor in adaption to changing environments. The projected climate change will be rapid on an evolutionary time scale, and any evolutionary adaptation will have to depend on the standing genetic variation. We examine these ideas in the following sections.
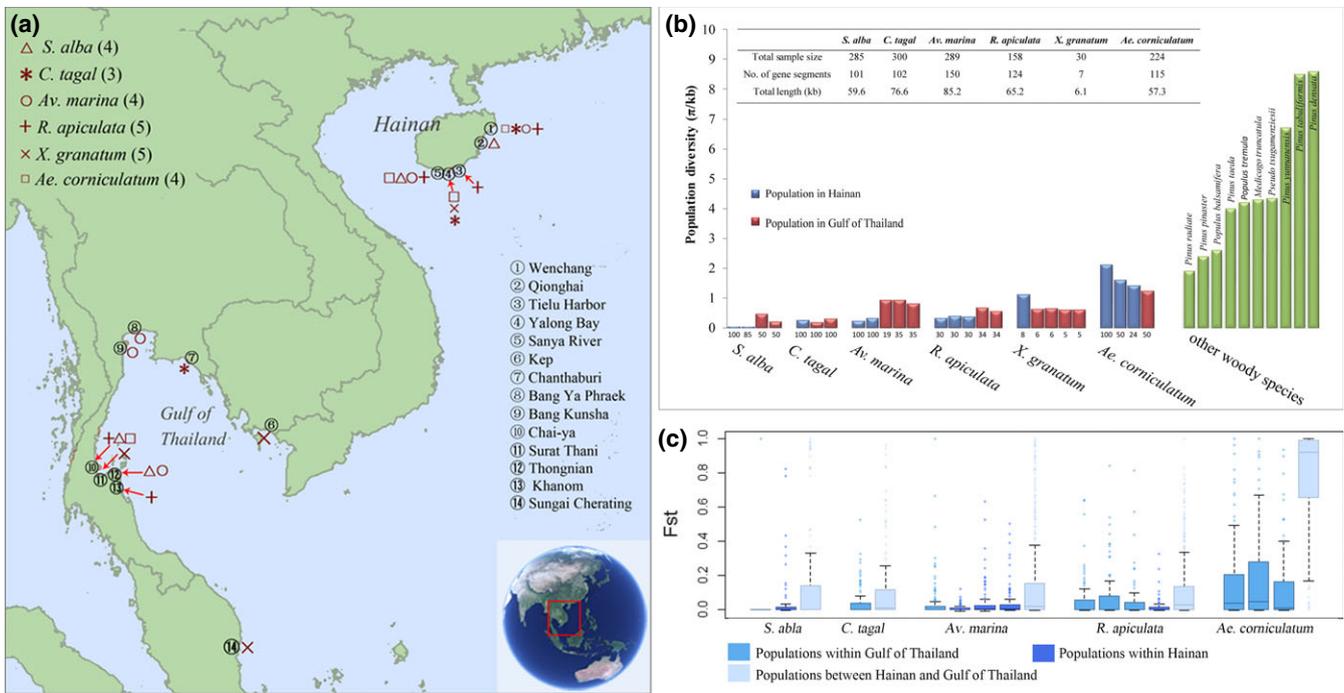
FIGURE 1 Genetic diversity in regional populations of six mangrove species. (a) Sampling locations. Species are indicated with different symbols, as listed in the top left corner, with the total population number of each species in brackets. (b) Each bar represents the π value in a population; populations on Hainan Island are in blue, and those on the coasts of the Gulf of Thailand are in red. Numbers under each bar represent sample sizes. Values for some woody plant relatives are also presented as green bars on the right for comparison. The nested table presents relevant sample statistics. (c) Each box represents F_{ST} between populations within the Gulf of Thailand and Hainan or between Hainan and the Gulf of Thailand

3.2 | Changes in the past effective population size

To test whether mangroves suffered reductions in effective population sizes over the last 20,000 years and whether these changes were correlated with the speed of sea level changes, we first plotted the sea level change over the last 100,000 years (Figure 2). Note that the crucial aspect is not the sea level itself but the rate of its fluctuation. It may take centuries of changes in sedimentation and soil chemistry for mangroves' habitats to become optimal for survival
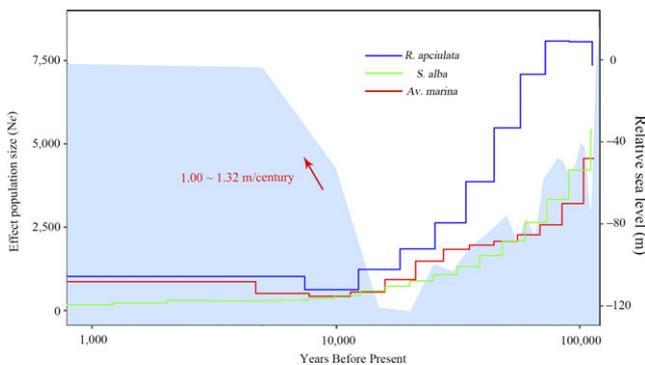

FIGURE 2 Demography of three mangrove species. Historical changes in effective population sizes (Ne, y-axis) going back in time (x-axis) inferred by the PSMC method. PSMC infers historical N_e changes from varying levels of genetic diversity in different DNA segments across the genome. *Rhizophora apiculata* is plotted in blue, *Sonneratia alba* in green, and *Avicennia marina* in red. Historical sea level fluctuations are plotted as the blue background

and reproduction. A rapid sea level change may dictate habitat shifts, either upland or down-coast. The sea levels rose by more than one metre per century between 18,000 and 6,000 years ago, and a slower (but still substantial) rate of change has also been recorded between 100,000 and 20,000 years before present.

With the geological data in hand, we inferred changes in the effective population sizes (N_e) of mangroves during the period in question using Pairwise Sequentially Markovian Coalescent (PSMC) analyses (Li & Durbin, 2011) on *S. alba*, *Av. marina*, and *R. apiculata* genomic sequences. The PSMC analyses suggest a common decrease in N_e for all three species during the most recent 20,000 years, coinciding with the dramatic sea level rise that was associated with the retreat of the latest glaciation (Figure 2). The reduction in N_e indicates that sea level changes during the Pleistocene glacial cycles caused a profound loss of genetic diversity among all of the mangrove species that we tested. Although the sea levels in the most recent 7,000 years have been stable in comparison with this long-term trend, it would take much longer than this for the genetic diversity to recover. The recent increase in the census population size is thus not yet reflected in the genetic measures of abundance.

3.3 | The dieback in Yalong Bay, China, in relation to water level rises

A test of a possible association of the extant genetic diversity and resistance to sea level fluctuations requires direct observations of

the effect of flooding on mangrove survival. An opportunity to conduct such a survey became available in 2010 (Figure 3). Yalong Bay in Hainan, China, has approximately 50 hectares of forest harbouring 13 true mangrove and seven semimangrove species (Zhong et al., 2009). It is part of a key mangrove reserve that boasts the largest and oldest *C. tagal* trees in China. The majority of mangrove trees in Yalong Bay are distributed along a river and lake that is approximately 1,500 m upstream of the estuary (Figure 3b). Between 2010 and 2012, the water level in Yalong Bay rose repeatedly due to a combination of human disturbance (chiefly the temporary narrowing

of the outlet during the construction of a resort close to the inlet) and an unusual abundance of rain (Fig. S1). There were at least three major, as well as many smaller, flooding incidents during that period (Fig. S1). The major floods resulted in elevated water levels of one metre or so. Each event lasted for approximately a week. The mangrove forest began to show large-scale dieback in mid-October 2011, continuing for more than 3 months (Figure 3a).

We assessed the extent of the dieback following the water level rise by comparing satellite images of the area before and after the event (Figure 3c). A change in canopy colour from green to brown
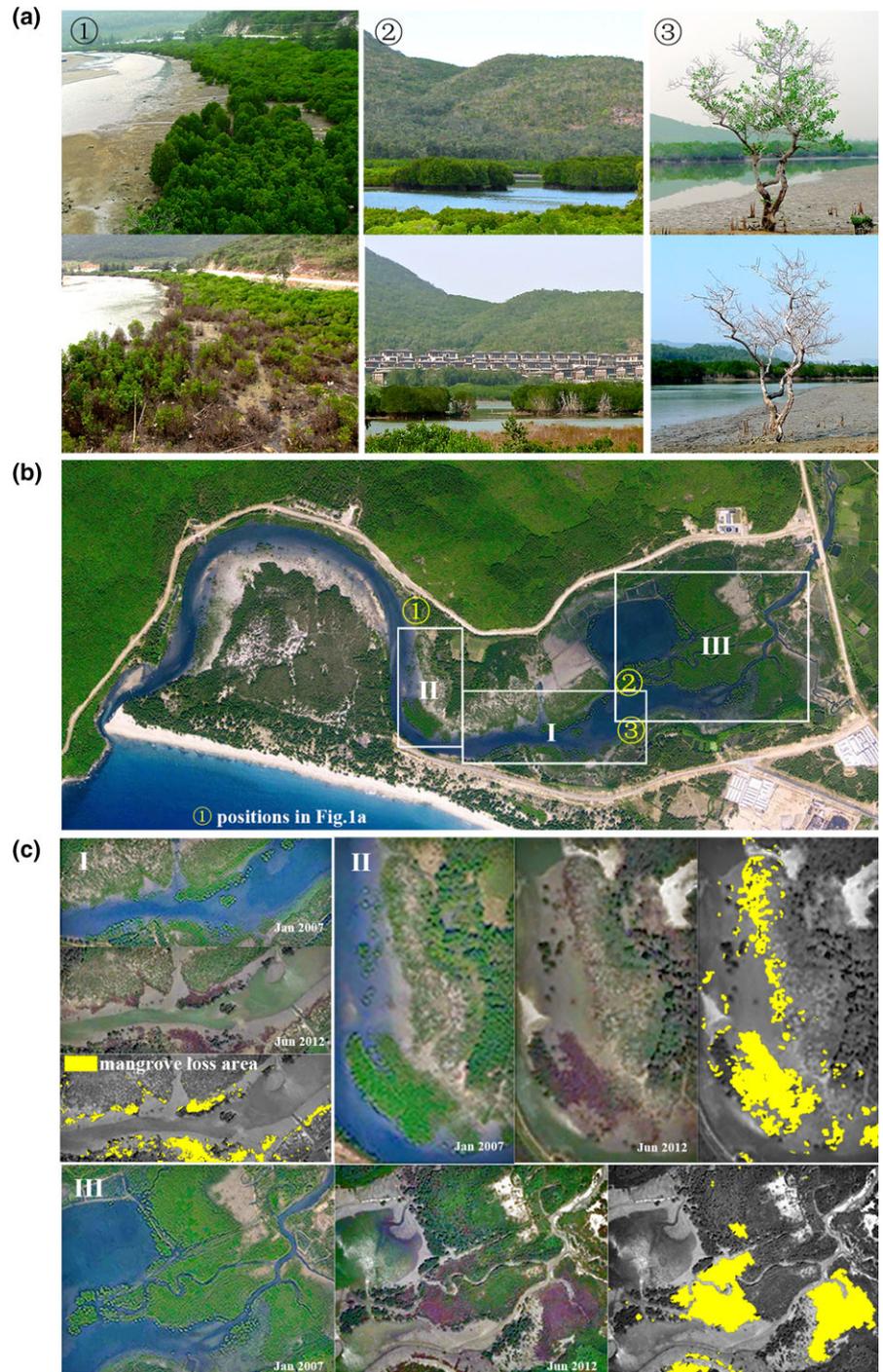

FIGURE 3 Satellite images and visual records of the mangrove dieback in Yalong Bay in 2010–2011. (a) Visual records comparing the mangrove tree conditions before and after the event in three locations (①, ②, and ③) indicated in panel b. (b) The mangrove distribution in Yalong Bay before the dieback event. (c) Satellite images of regions I, II, and III that are indicated in panel b. Healthy mangroves are in green and unhealthy mangroves are in dark purplish brown. Mangroves lost to the dieback event are depicted as yellow patches

TABLE 1 Field surveys of dominant mangrove species in Yalong Bay, Hainan, China after episodes of rising water in 2010–2012

Species	Number of trees surveyed	Proportion of trees affected (%, field survey in Jan 2012)			
		Healthy	Subnormal	Ill	Dead
Sonneratia alba	239	0	3.8	5	91.2
Ceriops tagal	3091	15.9	13.5	4.3	66.3
Avicennia marina	98	29.6	8.2	4.1	58.2
Rhizophora apiculata	1574	49.7	29.2	10	11.1
Xylocarpus granatum	161	85.7	11.8	1.9	0.6
Aegiceras corniculatum	421	89.5	10.5	0	0

or purple indicates mangrove death. To visualize the differences more clearly, we created contrasting images (see the yellow marking in Figure 3c), which indicated that half of the reserve was affected. If the dieback was a direct consequence of flooding, we would expect individuals at low elevations to be more significantly affected compared to trees occupying relatively high ground. We thus conducted surveys on *C. tagal* (the most affected species) along two transects (upstream and downstream) moving from the shoreline inland. We found that over 95% of *C. tagal* trees were dead at sites of low relative elevation, whereas trees on higher ground suffered much less (Fig. S2), consistent with our interpretation.

The severity of damage among mangrove species is quite heterogeneous (Table 1). Four species (*S. alba, C. tagal, Av. marina,* and *R. apiculata*) were severely affected, suffering a loss of 21–96% of living trees (Table 1). By contrast, *X. granatum* and *Ae. corniculatum* appeared to have survived well (Table 1). The genetic diversity of the six mangrove species (*S. alba, C. tagal, Av. marina, R. apiculata, X. granatum* and *Ae. corniculatum*) at the site and neighbouring locations was surveyed in 2008 and 2009, immediately before the dieback (see Figure 1). Most significantly, the local genetic diversity shows a strong negative correlation with the postflood mortality rate ($r = -.870$, $p = .024$; Figure 4). We also investigated whether the
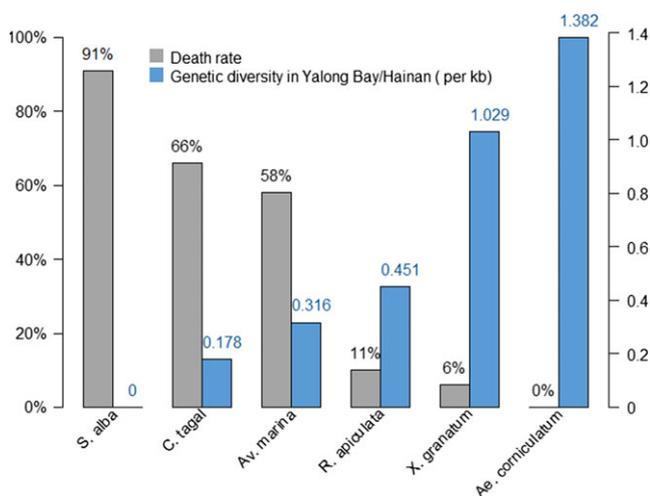
mangrove dieback had any effect on the rest of the ecosystem. Indeed, while we identified 35 species of molluscs at the site in 2009, only eight were found 2 years later (a 77% decline, Fig. S3). Similarly, fiddler crabs, iconic mangrove forest crustaceans, were once densely distributed in Yalong Bay, but only seven living individuals were found during a 6-day survey in February of 2012.

4 | DISCUSSION

The availability of genomic data boosts investigations of mangrove evolution and conservation. Using genome sequences of three typical mangroves, PSMC analyses revealed an N_e reduction during the past 100,000 years in concert with dramatic sea level change. This reduction hints that historic sea level changes had diminished the genetic diversity of mangroves even though these trees appear to be abundant in extant coastal forests. Intriguingly, the level of genetic diversity appears to be strongly correlated with the survival of mangroves during a recent water level rise in Yalong Bay. The low level of genetic diversity in mangroves is hence both a reflection of past performance and an indication of low genetic robustness against environmental change. The combined observations do not bode well for the long-term prospects for mangrove survival as sea levels rise.

Mangroves can adapt to rapid sea level elevation by vertical accretion of sediments or migration inland and along river deltas (Doyle et al., 2010). Sediment buildup, however, is only effective when sea levels do not rise too quickly. While this has been the case for the past 6,000 years, the current rate of change exceeds soil surface elevation gain in 69% of the sites examined in a recent study (Lovelock et al., 2015). Unfortunately, retreat to habitats that are currently inland can only happen in places that have not undergone human development. Such areas are becoming increasingly rare. Coastal wetlands are being rapidly reclaimed to construct industrial zones, ports, and other infrastructure (Ma et al., 2014). Seawalls cover up to 60% of the total coastline length in mainland China (Ma et al., 2014), directly hindering any landward migration by mangroves.

In contrast to other conservation efforts, protection of the present mangrove habitat will not suffice. Design of mangrove reserves must include buffer zones between mangrove forests and nearby developed lands. These buffer zones may at least delay submergence of coastal forests upon future sea level rise, perhaps enough for ecological acclimation to take place. Our results provide a glimpse into possible severe reductions in mangrove populations through climate change alone. Unless a careful plan is worked out to manage human development near mangrove forests, a world without mangroves (Duke et al., 2007) will be a distinct possibility in the 22nd century.

FIGURE 4 Field survey mortality and population genetic diversity of six Hainan Island mangrove species. The axis on the left indicates the death rate; that on the right indicates genetic diversity

AUTHOR CONTRIBUTIONS

S. S. supervised the project. Z. G., X. L. and Z. H. analysed the data and wrote the manuscript. X. L., Y. Y., W. W., C. Z. and S. S. performed the field surveys. A. G., C. W and N. D helped in preparing the manuscript.

COMPETING INTERESTS

The authors declare no competing financial interests.

DATA AVAILABILITY

Rhizophora apiculata, *Avicennia marina* and *Sonneratia alba* resequencing data used for PSMC analyses can be obtained from the NCBI Sequence Read Archive with BioSample codes SAMN04161419, SAMN04161417 and SAMN04161433, respectively. Short read sequences from *S. alba*, *Ceriops tagal*, *Aegiceras corniculatum*, *Av. marina*, and *R. apiculata* were also deposited in the NCBI Sequence Read Archive, BioProject: PRJNA303892.

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REFERENCES

Alongi, D. M. (2015). The impact of climate change on mangrove forests. *Current Climate Change Reports*, 1, 30–39. https://doi.org/10.1007/s40641-015-0002-x

Barbier, E. B., Hacker, S. D., Kennedy, C., Kock, E. W., Stier, A. C., & Sillman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81, 169–193. https://doi.org/10.1890/10-1510.1

Bilmes, J. A. (1998). A gentle tutorial of the EM algorithm and its application to parameter estimation for gaussian mixture and hidden markov models. *ReCALL*, 4, 126.

Chen, Y., Hou, Y., Guo, Z., Wang, W., Zhong, C., Zhou, R., & Shi, S. (2015). Applications of multiple nuclear genes to the molecular phylogeny, population genetics and hybrid identification in the mangrove genus *Rhizophora*. *PLoS ONE*, 10, 1–17. https://doi.org/10.1371/journal.pone.0145058

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., . . . Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26, 152–158. https://doi.org/10.1016/j.gloenvcha.2014.04.002

Dempster, A. P., Laird, N. M., & Rubin, D. B. (1977). Maximum likelihood from incomplete data via the EM algorithm. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, 39, 1–38.

DePristo, M. A., Banks, E., Poplin, R., Garimella, K. V., Maguire, J. R., Hartl, C., . . . Daly, M. J. (2011). A framework for variation discovery and genotyping using next-generation DNA sequencing data. *Nature Genetics*, 43, 491–498. https://doi.org/10.1038/ng.806

Doyle, T. W., Krauss, K. W., Conner, W. H., & From, A. S. (2010). Predicting the retreat and migration of tidal forests along the northern Gulf of Mexico under sea-level rise. *Forest Ecology and Management*, 259, 770–777. https://doi.org/10.1016/j.foreco.2009.10.023

Duke, N. C., Kovacs, J., Griffiths, A., Preece, L., Hill, D. J., Van Oosterzee, P., . . . Burrows, D. (2017). Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: A severe ecosystem response, coincidental with an unusually extreme weather event. *Marine and Freshwater Research*, 68(10), 1816–1829. https://doi.org/10.1071/MF16322

Duke, N. C., Meynecke, J. O., Dittmann, S., Ellison, A. M., Anger, K., Berger, U., . . . Koedam, N. (2007). A world without Mangroves? *Science*, 317, 41–43. https://doi.org/10.1126/science.317.5834.41b

Guo, Z., Huang, Y., Chen, Y., Duke, N. C., Zhong, C., & Shi, S. (2016). Genetic discontinuities in a dominant mangrove *Rhizophora apiculata* (Rhizophoraceae) in the Indo-Malesian region. *Journal of Biogeography*, 43, 1856–1868. https://doi.org/10.1111/jbi.12770

Huang, Y., Zhu, C., Li, X., Hu, L., Li, X., Tan, F., . . . Shi, S. (2012). Differentiated population structure of a genetically depauperate mangrove species *Ceriops tagal* revealed by both Sanger and deep sequencing. *Aquatic Botany*, 101, 46–54. https://doi.org/10.1016/j.aquabot.2012.04.001

IPCC (2013) *"Climate Change 2013: The Physical Science Basis"* (Workgroup I, 2013).

Krauss, K. W., Mckee, K. L., Lovelock, C. E., Cahoon, D. R., Saintilan, N., Reef, R., & Chen, L. (2014). How mangrove forests adjust to rising sea level. *New Phytologist*, 202, 19–34. https://doi.org/10.1111/nph.12605

Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics*, 25, 1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Li, H., & Durbin, R. (2011). Inference of human population history from individual whole-genome sequences. *Nature*, 475, 493–496. https://doi.org/10.1038/nature10231

Li, H., Ruan, J., & Durbin, R. (2008). Mapping short DNA sequencing reads and calling variants using mapping quality scores. *Genome Research*, 18, 1851–1858. https://doi.org/10.1101/gr.078212.108

Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., . . . Saintilan, N. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature*, 526, 559–563. https://doi.org/10.1038/nature15538

Ma, Z., Melville, D. S., Liu, J., Chen, Y., Yang, H., Ren, W., . . . Li, B. (2014). Rethinking China's new great wall. *Science*, 346, 912–914. https://doi.org/10.1126/science.1257258

Mcgranahan, G., Balk, D., & Anderson, B. (2007). The rising tide: Assessing the risks of climate change and human settlements in low elevation coastal zones. *Environment and Urbanization*, 19, 17–37. https://doi.org/10.1177/0956247807076960

Mckee, K. L., Cahoon, D. R., & Feller, I. C. (2007). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, 16, 545–556. https://doi.org/10.1111/geb.2007.16.issue-5

Nei, M., & Li, W.-H. (1979). Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences of the United States of America*, 76, 5269–5273. https://doi.org/10.1073/pnas.76.10.5269

Urashi, C., Teshima, K. M., Minobe, S., Koizumi, O., & Inomata, N. (2013). Inferences of evolutionary history of a widely distributed mangrove species, *Bruguiera gymnorrhiza*, in the Indo-West Pacific region. *Ecology and Evolution*, 3, 2251–2261. https://doi.org/10.1002/ece3.624

Van der Auwera, G. A., Carneiro, M. O., Hartl, C., Poplin, R., del Angel, G., Levy-Moonshine, A., . . . Banks, E. (2013). From fastQ data to high-confidence variant calls: The genome analysis toolkit best practices pipeline. *Current Protocols in Bioinformatics*, 43, 11.10.1–11.10.33. https://doi.org/10.1002/0471250953.bi1110s43

Wee, A. K. S., Takayama, K., Chua, J. L., Asakawa, T., Meenakshisundaram, S. H., Adjie, B., . . . Salmo, S. G. (2015). Genetic differentiation and phylogeography of partially sympatric species complex *Rhizophora mucronata* Lam. and *R. stylosa* Griff. using SSR markers. *BMC Evolutionary Biology*, *15*, 57. https://doi.org/10.1186/s12862-015-0331-3

Xu, S., He, Z., Guo, Z., Zhang, Z., Wyckoff, G. J., Greenberg, A., . . . Shi, S. (2017). Genome-wide convergence during evolution of mangroves from woody plants. *Molecular Biology and Evolution*, *34*, 1008–1015. https://doi.org/10.1093/molbev/msw277

Xu, S., He, Z., Zhang, Z., Guo, Z., Guo, W., Lyu, H., . . . Zhou, R. (2017). The origin, diversification and adaptation of a major mangrove clade (Rhizophoreae) revealed by whole genome sequencing. *National Science Review*, *4*, 1–20. https://doi.org/10.1093/nsr/nwx065

Yang, Y., Li, J., Yang, S., Li, X., Fang, L., Zhong, C., . . . Shi, S. (2017). Effects of Pleistocene sea-level fluctuations on mangrove population dynamics: A lesson from *Sonneratia alba*. *BMC Evolutionary Biology*, *17*, 22. https://doi.org/10.1186/s12862-016-0849-z

Zhong, C., Lin, G., Chen, Y., Xue, J., Fu, R., & Mai, L. (2009). A community survey to mangrove forest in the Qingmei harbour, Sanya. *Tropical Forestry*, *37*, 45–47.

Zhou, R., Ling, S., Zhao, W., Osada, N., Chen, S., Zhang, M., . . . Lu, X. (2011). Population genetics in nonmodel organisms: II. Natural selection in marginal habitats revealed by deep sequencing on dual platforms. *Molecular Biology and Evolution*, *28*, 2833–2842. https://doi.org/10.1093/molbev/msr102

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